Environmental factors affecting the wintering raptor community in Armenia, Southern Caucasus

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Abstract
The species–habitat relationships can change during the year because of the seasonality of resources. Therefore, the investigation of habitat use by animals in each season plays a fundamental role in their conservation. The main aim of this research was to investigate the raptor community that spends the winter in Armenia, southern Caucasus, and to explore its relationship with environmental features, such as land use and topography. During January 2012, we collected data by carrying out 15 roadside counts along which we calculated three community parameters: the relative abundance, the species richness, and the species diversity. Then, we carried out a multiple linear regression with the Information-Theoretic Approach, to explain the relationship between the parameters and environmental variables. Besides, we computed a Canonical Correspondence Analysis (CCA) between the species and the environment around their observations. As a general pattern, the community was associated with permanent crops, maybe because of their heterogeneity, which in turn allows them to support higher densities of prey during the winter. The most abundant species was the Black Kite (Milvus migrans), followed by the Common Kestrel (Falco tinnunculus) and the Griffon Vulture (Gyps fulvus). To our knowledge, this is one of the first studies investigating the wintering raptor community in the Caucasus, with raptors generally studied in this area during the breeding season and migration.

Keywords Birds of prey · Canonical Correspondence Analysis · Habitat use · Kilometric abundance index · Permanent crops

Introduction
Biodiversity preservation and restoration are the most important goals of conservation biology, and to apply adequate management schemes for the conservation of animals, the ecology and habits of each species should be known (Sinclair et al. 2006; Macdonald and Service 2007). Currently, the main variable used to understand and predict species distribution is habitat type (Guisan et al. 2017). The basis of species–habitat relationships lies in habitat selection (Manly et al. 2002; Morrison et al. 2006), a process by which an individual must choose the habitats where it can live. These choices are influenced by a variety of constraints, such as the abundance and distribution of resources in both time and space, the distribution of conspecifics and predators, among others (Manly et al. 2002; Morrison et al. 2006). Species–habitat relationships are also intimately linked to the concept of the niche (Morrison et al. 2006). Hutchinson (1957) defined the niche as a hyper-volume in the multi-dimensional space of ecological variables, within which a species can maintain a viable population. In this view, niche dimensions are represented by multiple environmental gradients. A given species (or population) can exist in only a subset of the conditions defined by all the gradients (its potential or fundamental niche) but maybe further restricted in distribution (its realized niche) by predators and competitors. Indeed, in line with Gause principle (Gause 1934), stable populations of two species sharing the same niche cannot coexist in the same area; they must differ at least in one

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niche dimension (Amarasekare 2003). Species–habitat relationships can be investigated by habitat suitability models to define the potential response of a species to habitat availability, to produce predictive maps of its potential distribution, and to describe the characteristics of its niche (Guisan and Zimmermann 2000; Boice et al. 2002; Chiatante 2019). Hence, this tool is very important for management purposes (Bayliss et al. 2005). Species–habitat relationships can change during the year because of the seasonality of resources (Manly et al. 2002; Morrison et al. 2006), and because many species change their distribution depending on the season, which sometimes involves migrations (Dingle 1996; Hansson and Åkesson 2014). In this case, the whole community change in a year more or less evidently and the species sometimes modify their requirements to coexist with others (Caula et al. 2008; Chen et al. 2011; Kwieciński et al. 2016; Yabuhara et al. 2019). Undoubtedly, birds are among the most mobile animals and their communities change seasonally (Rotenberry et al. 1979; Cody 1985), which involves some consequences. For example, during the breeding and non-breeding seasons migrants enrich the resident communities of birds, with consequent competition for space and food between them (Herrera 1978; Telléría and Pérez-Tris 2003; Wilson and Cresswell 2007). However, in some cases there is a positive interaction between species: in fact, the migrant can use the resident as a cue to assess habitat quality (Mönkkönen et al. 1999; Mönkkönen and Forsman 2002).

Habitat use of diurnal raptors has been poorly studied in winter, but they seem to be influenced mainly by food availability (Newton 1979) and, consequently, it is driven by their hunting strategies (Jankowiak et al. 2015b). Indeed, as for raptors, also prey species are spatially distributed in relation to their ecological requirements. Moreover, land use and the environmental structure affected the hunting success of raptors (Palatitz et al. 2015; Jaramillo et al. 2016) and prey availability is a primary element determining the size of their territories (Martínez-Hesterkamp et al. 2018). Despite the gap of knowledge, some researches give us some useful information for habitat use in winter by raptors. For example, Golden Eagle (Aquila chrysaetos) home ranges in winter were primarily composed of forest and open habitat (Miller et al. 2017), whereas Northern Goshawk (Accipiter gentilis) uses deciduous and conifer forests (Tornberg and Colpaert 2001). Prairie Falcons (Falco mexicanus), Ferruginous Hawks (Buteo regalis), and Rough-legged Buzzards (Buteo lagopus) inhabit natural grasslands of North America (Ingold 2010; Pandolfino et al. 2011), while Montagu’s Harriers (Circus pygargus) were observed hunting in the savannah during the winter (Augiron et al. 2015). Yet, Bald Eagle (Haliaeetus leucocephalus) is positively associated with wetlands (Pandolfino et al. 2011), as well as Greater Spotted Eagle (Clanga clanga) (Pérez-García et al. 2014). In Europe, agricultural areas, especially the non-intensive, are used mainly by Common Buzzards (Buteo buteo) (Nikolov et al. 2006; Baltag et al. 2013; Panuccio et al. 2019a) and Common Kestrels (Falco tinnunculus) (Palomino Nantón 2011), which base their winter diet especially on voles (Zmihorski and Rejt 2007; Francksen et al. 2016). Particularly, Common Buzzards uses mainly permanent papilionaceous crops (e.g. lucerne, clover), cereal stubbles (including maize stubbles), and meadows (Wuczyński 2005). Likewise, American Kestrel (Falco sparverius), Northern Harrier (Circus hudsonianus), and White-tailed Kite (Elanus leucurus) occur in North American farmlands (Pandolfino et al. 2011). In general, both the diversity and abundance of raptors during the winter decrease when the proportion of urban areas is high (Palomino and Carrascal 2007; Jankowiak et al. 2015b; Panuccio et al. 2019b). In some cases, the adults spend the winter in their nesting territories occupying the same hunting ranges all the year, whereas in others they leave and disperse locally or on a long migration. These strategies may represent a progressive adaptation to decreasing availability of prey in winter (Newton 1979). However, some studies have pointed out that although prey are available, the wintering raptor density is limited by a shortage of perching and roosting sites, especially in open landscapes (Wuczyński 2005; Ingold 2010). Among raptors breeding in the Western Palearctic, 13 are trans-Saharan migrants that overwinter south of the Sahara, in the Sahel or tropical Africa, 17 have wintering grounds closed to their breeding territories, as the Mediterranean Basin and in western Asia, whereas 10 species winter partly in both regions (Newton 1979). This division may reflect dietary requirements, in as much as the species that remain in Europe and near the nesting territories have diets based on warm-blooded prey. This is in contrast with the long-distance migrant species that are insect-, reptiles-, and fish-eaters (Newton 1979; Ferguson-Lees and Christie 2001). In addition, raptors may benefit from wintering close to their breeding grounds through a reduction in migratory costs, allowing an early arrival in the nesting territory, which in turn is positively correlated with the breeding success (Espie et al. 2000; Steenhof and Heath 2013; Paprocki et al. 2015).

This research aimed to investigate the relationships between the wintering raptor community and the environment (such as land use and topography) in the southern Caucasus, particularly in Armenia, in western Asia. Southern Caucasus holds a high species richness of raptors; indeed, 40 species have been recorded, including resident, breeding, wintering, migrating, and vagrant species (Abuladze 2013). Among the breeding species, Common Buzzards and Common Kestrel are the most widespread species, with up to 1000 and 5000 breeding pairs, respectively, followed by the Lesser Kestrel (Falco naumanni) and the Levant Sparrowhawk (Accipiter brevipes), which, however, are mainly localized in Azerbaijan (where 1500–3000 and 500–1000
pairs breed, respectively) (BirdLife International 2015). Specifically, in Armenia the most abundant species is the Common Kestrel (250–400 pairs), followed by the Common Buzzard (100–150 pairs), the Eurasian Sparrowhawk (Accipiter nisus) (100–150), and the Lesser Kestrel (100–130 pairs) (BirdLife International 2015).

Moreover, Caucasus has special importance for migrating raptors because it is located on the crossroads between Europe and Asia and between breeding and wintering quarters of many species. The most important flyway is undoubtedly that of the Eastern Black Sea, with the Batumi bottleneck in Georgia (up to more than 1,000,000 individuals of 34 species) (Verhelst et al. 2011; Wehmann et al. 2019). However, there are also other important flyways, such as the Mtkvari valley (up to 250,000 individuals of 26 species), Alazani (150,000–200,000 individuals of 24 species), and Javakheti (up to 200,000 individuals of 25 species) (Abuladze 2013). On the western Caspian coast, migrating raptors have mainly been studied along the shoreline of Dagestan (Russia) (Butiev et al. 1983; Kostin and Butiev 2000), even though these regions are known mainly for the migration of waders and other birds, especially at the Besh Barmag bottleneck in Azerbaijan (Shubin 1998; Heiss 2013; Heiss et al. 2020). On the other hand, during the winter 23 species occur, 18 of which are regular visitors and their number fluctuated between 4400 and 14,700 birds depending upon climatic conditions (Abuladze 2013). Generally, they inhabit areas with high prey availability and with no or little snow cover, up to 600 m above sea level and with heterogeneous landscapes. In Georgia, the most numerous species are by far the Black Kite (Milvus migrans), especially in the Kolkheti Lowland, with 3000–12,000 individuals, and the Hen Harrier (Circus cyaneus), with 600–1700 individuals (Abuladze 2013). Our study is important for at least two reasons. First, there are few studies related to wintering birds of prey in the Caucasus (Gavashelishvili et al. 2012; Abuladze 2013), despite the area hosting a fundamental route for raptor migration. Secondly, to the best of our knowledge, this is the first research concerning the wintering raptor community in Armenia, being the most research concerning the breeding community (Aghababyan 2006; Ananian 2009; Ananian et al. 2010, 2011).

**Materials and methods**

**Study area**

The study area was located on the southern slope of Caucasus (44°17.10′ E, 40°10.54′ N), in particular in the provinces of Shirak, Aragatsotn, Armavir, Kotayk, Ararat, and in the municipality of Yerevan, in central-western Armenia (Fig. 1). The landscape is characterized by mountains with an average altitude of 1719 m a.s.l. (the highest peaks are Kakhamakhut at 2106 m a.s.l. and Mets Artenis at 2047 m a.s.l.). The climate is arid and continental with warm summers and cold winters, average annual precipitation of 200–600 mm, and an average annual temperature of 3–13 °C. The land use is mainly characterized by pastures (59.8%) and arable lands (20.7%), followed by built-up areas (6.8%) and forests/shrublands (4.2%).

**Data collection**

Roadside surveys were carried out using the car transect method (Andersen et al. 1985; Millsap and LeFranc 1988; Viñuela 1997), by carrying out 15 transects at low speed (20–40 km/h) once in January 2012, for an average length of 31.5 km each and a total of 466 km. Transects were chosen to cover almost evenly the study area (Fig. 1). The perpendicular distance from the observer to each bird sighted was estimated to locate exactly its position. To do this, we required two measurements: (1) the distance between the observer and the bird and (2) the angle between the transect axis and the bird, which were taken with a rangefinder (Leica Rangemaster CRF 1600B, 7 × 24, error ± 1 m; Leica, Solms, Germany) and a compass. Each observation was geolocalized using a Garmin Colorado 300 GPS (Garmin, Olathe, KS, USA). Other than relevant data (i.e. species, date/time, perpendicular distance from transect, coordinates of observation), we recorded also ancillary information on the bird, such as sex/age and behaviour. Birds flying over that had not taken off from or landed in the site were not included (Bibby et al. 2000). All counts were carried out on calm days with no precipitation.

**Environmental variables**

Land use was obtained by combining two heterogeneous datasets (Rosina et al. 2018). In particular, the land use map developed by Scientific Network for the Caucasus Mountains Region (SNC-mt) (Debarbieux et al. 2015; Adler et al. 2018) (available at http://sustainable-caucasus.unepgrid.ch/) was updated by the vector layers (forests, human settlements, lakes and wetlands, and cliffs) provided by the Acopian Center for the Environment (ACE) (available at https://ace.aua.am/gis-and-remote-sensing/vector-data). The validation of the combined land cover map was based on the visual interpretation of high-resolution images on Google Earth (© Google LLC; available at https://www.google.com/earth/index.html) at 300 locations randomly selected in the study area (Dorais and Cardille 2011; Zhao et al. 2014). In this way, a more reliable map was obtained, with only 6.5% of misclassification. Geomorphological data were obtained from ALOS Global Digital Surface Model (© JAXA) with
a spatial resolution of 30 m. Spatial data were processed by the software Quantum GIS v.3.2.3 ‘Bonn’.

Statistical analysis

First, the relative abundances of both each species and all raptors were assessed along each transect by Kilometric Abundance Index (KAI), i.e. the number of birds observed per transect length. This simple but valuable relative measure has been used in many studies on raptors because abundances among transects can be compared easily (Carrete et al. 2009; Palomino Nantón 2011; Paz et al. 2013). Moreover, it is very appropriate for assessing bird abundances in open country, as in our study, because of the bias of roadside surveys in favour of open areas, grasslands, and arable lands (Millsap and LeFranc 1988; Harris and Haskell 2007).

To assess the relationship between the community of raptors and the environment, the KAI of all raptors was related to seven environmental variables (Table 1), measured in a buffer of 500 m around transects, by multiple linear regression analysis (Legendre and Legendre 1998). We chose a buffer of 500 m because it was used in similar researches concerning wintering raptors (Ingold 2010; Pandolfino et al. 2011; Jankowiak et al. 2015b). Besides, both the species richness (calculated as the number of species observed along each transect) and the species diversity, quantified by the Shannon Diversity Index (Magurran and McGill 2011), were used as response variables. Then, a set of a priori models

![Figure 1](https://example.com/image1.png)

**Fig. 1** Study area and the transects carried out to investigate the spatial distribution of wintering raptors in central-western Armenia during the winter of 2012

| Environmental variables               | Mean ± SE | Min–max   |
|---------------------------------------|-----------|-----------|
| Urban settlements (% cover)            | 19.6 ± 4.50 | 5.0–70.1  |
| Arable lands (% cover)                 | 24.7 ± 6.56 | 0.0–80.1  |
| Permanent crops (% cover)              | 9.2 ± 2.54  | 0.0–27.0  |
| Pastures (% cover)                     | 43.8 ± 6.75 | 0.5–91.6  |
| Lakes and reservoirs (% cover)         | 1.0 ± 0.62  | 0.0–9.2   |
| Density of rivers (m/ha)               | 34.9 ± 7.54 | 1.9–121.9 |
| Mean altitude (m. a.s.l.)              | 1025 ± 56.61 | 827–1589 |

The values were derived from the 500-m buffers around transects.
was built, for each model both AICc and Akaike weights (\(w_i\)) were calculated, and the models were ranked by the differences with minimum AICc (\(\Delta AICc\)) (Burnham and Anderson 2002). Models with \(\Delta AICc \leq 2\) were considered the best ones; therefore, they were used to compute model averaging; otherwise only the best model was selected for predictions and further analyses (Burnham and Anderson 2002). Finally, we measured the relative importance of variables \(w\) by the sum of Akaike weights of the models in which each variable appeared (Burnham and Anderson 2002). For the analyses, all the considered variables were standardized by normalization, that is, each variable had a mean of zero and a standard deviation of one (Zuur et al. 2007). The Variance Inflation Factor (VIF) with a threshold of 3 was used to exclude the variables collinearity (Fox and Monette 1992; Zuur et al. 2010). The model’s performance was tested through Pearson’s correlation between observed and predicted values (Legendre and Legendre 1998). Moreover, the model’s residuals were calculated and tested for normality by Kolmogorov–Smirnov test and spatial correlation by Moran I test; the coefficient of determination \(R^2\) was used as a measure of the variation explained by models (Zuur et al. 2007; Bivand et al. 2008).

Subsequently, a Canonical Correspondence Analysis (CCA) was carried out to examine the relationships between species and the percentage cover of land use in a circular buffer of 500 m around each observation. Canonical Correspondence Analysis is a multivariate constrained ordination technique, frequently used in ecology (Ter Braak 1986; Hill 1991; Guisan and Zimmermann 2000). To build the model and to test the significance of the variables, the ANOVA-like permutation test with 1000 replications was applied (Borcard et al. 2011; Kmecl and Denac 2018). To test for multivariate collinearity, the VIF was measured for the analysis with a threshold of 3 (Zuur et al. 2010). The spatial autocorrelation in residuals was tested with a geostatistical form of multi-scale ordination, which uses a variogram matrix to partition CCA results by distance (Wagner 2003, 2004; Couteron and Ollier 2005; Legendre and Gauthier 2014). In practice, this variogram plots the inertia profiles against distance and hence can be used to identify statistically uncorrelated patterns represented by the ordination axes (Wagner 2003, 2004; Couteron and Ollier 2005; Legendre and Gauthier 2014). Therefore, an empirical variogram of the inertia was calculated with distance classes of 1 m, and a significance test for spatial autocorrelation of the residual inertia was performed for each distance class using a Mantel test with 1000 permutations (Wagner 2004; Borcard and Legendre 2012).

**Results**

During fieldwork, 168 raptors of 10 species were counted (Table 2). The Common Kestrel was the most widespread species, which was observed on 10 transects out of 15.

| Species                          | T2 | T3 | T4 | T6 | T7 | T8 | T9 | T10 | T11 | T12 | T13 | T15 | KAI±SE       |
|----------------------------------|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-------------|
| Cinereous Vulture Aegypius monachus | –  | –  | –  | –  | 1  | –  | –  | –   | –   | –   | –   | 5   | 0.010±0.008 |
| Griffon Vulture Gyps fulvus       | –  | –  | –  | –  | 1  | 5  | 12 | –   | –   | –   | –   | 3   | 0.034±0.020 |
| Black Kite Milvus migrans        | –  | 8  | 57 | –  | –  | 1  | –  | –   | –   | –   | –   | –   | 0.674±0.611 |
| Western Marsh Harrier Circus aequinosis | –  | 1  | 4  | –  | –  | 3  | –  | –   | –   | –   | –   | –   | 0.053±0.043 |
| Hen Harrier Circus cyaneus        | –  | –  | 1  | –  | –  | 2  | –  | 5   | –   | –   | –   | –   | 0.018±0.011 |
| Common Buzzard Buteo buteo        | –  | –  | 1  | 2  | –  | 2  | –  | –   | 5   | –   | –   | –   | 0.019±0.012 |
| Long-legged Buzzard Buteo rufinus | –  | –  | 1  | –  | –  | 1  | –  | –   | –   | –   | –   | –   | 0.012±0.011 |
| Eurasian Sparrowhawk Accipiter nisus | 1  | 1  | –  | –  | 1  | 1  | –  | –   | –   | –   | –   | –   | 0.016±0.011 |
| Northern Goshawk Accipiter gentilis | –  | –  | –  | –  | –  | –  | –  | –   | –   | –   | –   | –   | 0.001±0.001 |
| Common Kestrel Falco tinnunculus  | 1  | 1  | 2  | 4  | 8  | 7  | 2  | 4   | 3   | 13  | 2   | 10  | 0.075±0.016 |
| Total                           | 2  | 10 | 65 | 4  | 4  | 1  | 1  | 16  | 7   | 18  | 3   | 18  | 0.361±0.687 |

For each species, the number of individuals is shown, as well as the average Kilometric Abundance Index (KAI). Transects (Ts) without observations (i.e. T1, T5, and T14) are not shown.
followed by Eurasian Sparrowhawk and Griffon Vulture, both detected on four transects. The average KAI showed that the Black Kite was the most abundant species, followed by the Common Kestrel and the Western Marsh Harrier (Table 2).

For the KAI, only one model entered in the best set of models ($w_i=0.93$); therefore, we used only this for further analyses. The KAI of all raptors was positively associated with the cover of permanent crops and the mean altitude along transects (Tables 3, 4; Electronic Supplementary Materials, ESM Table S1; Fig. 2). There was no collinearity between selected variables (see Table 4) and predicted abundances were strongly correlated with observed values ($r=0.892$, $P<0.001$). The residuals model were normally distributed ($D=0.135$, $P=0.948$) and non-spatially correlated ($I=0.824$, $P=0.341$); this model explained 75.4% of variance.

For the species richness, the sum of Akaike weights of the three best models was equal to 0.51, whereas for the species diversity was equal to 0.50. Based on these results, we assessed that for both these response variables, there was only weak evidence for the importance of environmental variables. However, similar to abundance, both the species richness and diversity seemed to have a positive relationship with the cover of permanent crops. Also, for species richness, the mean altitude along transects would appear to have a positive effect (Tables 3, 4; ESM Table S2–S3; Fig. 2). Contrarily, the density of rivers would seem to affect negatively species diversity (Table 4). There was no collinearity between selected variables (Table 4) and predicted values were significantly correlated with observed values (for the species richness, $r=0.553$, $P=0.049$; for the species diversity, $r=0.593$, $P=0.033$). Model residuals were normally distributed and non-spatially correlated both for the species richness ($D=0.251$, $P=0.330$; $I=−0.731$, $P=0.768$) and the species diversity ($D=0.148$, $P=0.899$; $I=−0.407$, $P=0.658$). The variance explained was comprised between 21 and 37% for the species richness, whereas it is between 18 and 21% for the species diversity.

The CCA showed how the 10 species fitted into the ordination space (Table 5, Fig. 3). The permutation test showed that both the global CCA model and the first axis explained a significant amount of variation in observed species

| Table 3 | Best set of models ($\Delta AIC_c \leq 2$) explaining the occurrence of wintering raptors in Armenia |
|---------|----------------------------------------------------------------------------------------------------------------|
| Response | Environmental variables | $df$ | logLik | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ |
| KAI     | Altitude + permanent crops | 4   | 19.62  | −26.20 | − | 0.928 | 0.75 |
| Species richness (Intercept) | 2  | −26.51  | 58.20  | 0.00  | 0.228 | − |
| Permanent crops | 3  | −24.99  | 58.60  | 0.44  | 0.183 | 0.21 |
| Altitude + permanent crops | 4  | −23.49  | 60.00  | 1.76  | 0.094 | 0.37 |
| Species diversity (Intercept) | 2  | 1.61  | 2.00  | 0.00  | 0.200 | − |
| Density of rivers | 3  | 3.13  | 60.00  | 1.76  | 0.094 | 0.37 |
| Permanent crops | 3  | 2.93  | 2.80  | 0.82  | 0.133 | 0.21 |

For each model, the degrees of freedom ($df$), the log-likelihood (logLik), the $AIC_c$, and the difference with the minimum $AIC_c (\Delta AIC_c)$, the Akaike weight ($w_i$), and the coefficient of determination $R^2$ are shown

| Table 4 | Average models explaining the environmental requirements of wintering raptors in Armenia during the winter of 2012 |
|---------|---------------------------------------------------------------------------------------------------------------|
| Environmental variable | $\beta$ | SE | LCI | UCI | $w$ | VIF |
| KAI (Kilometric Abundance Index) | | | | | | |
| Intercept | 0.159 | 0.017 | – | – | – | – |
| Permanent crops (%) | 0.125 | 0.020 | 0.080 | 0.170 | 1.00 | 1.312 |
| Mean altitude (m a.s.l.) | 0.074 | 0.020 | 0.029 | 0.119 | 1.00 | 1.312 |
| Species richness | | | | | | |
| Intercept | 2.077 | 0.572 | – | – | – | – |
| Permanent crops (%) | 1.031 | 0.635 | −0.213 | 2.275 | 0.55 | 1.087 |
| Mean altitude (m a.s.l.) | 0.897 | 0.631 | −0.341 | 2.134 | 0.19 | 1.087 |
| Species diversity (Shannon Index) | | | | | | |
| Intercept | 0.233 | 0.066 | – | – | – | – |
| Permanent crops (%) | 0.095 | 0.068 | −0.233 | 0.029 | 0.33 | – |
| Density of rivers | −0.102 | 0.067 | −0.038 | 0.229 | 0.27 | – |

The estimate ($\beta$), the standard error (SE), the lower (LCI) and upper (UCI) 95% confidence intervals, the relative importance of the variable ($w$), and the Variance Inflation Factors (VIF) are shown. For species diversity, the VIF was not calculated because all models had only one variable.
abundances (global model: $F = 2.037, P = 0.021$; CCA1: $F = 6.515, P = 0.009$). Only the per cent cover of lakes and reservoirs contributed significantly to the observed variation in species abundances ($F = 5.913, P = 0.001$). Cliffs and rocks ($F = 1.093, P = 0.288$), permanent crops ($F = 1.589, P = 0.126$), pastures ($F = 0.537, P = 0.847$), and urban settlements ($F = 1.053, P = 0.316$) were not significant. Of the total inertia (variance), only 11.4% was explained by the predictors and 64.0% of this value was explained by the first axis. This axis was positively correlated with lakes and reservoirs, whereas negatively with pastures and urban settlements. Relationships between species and environmental predictors could be discerned from the biplot (Fig. 3): the Western Marsh Harrier was associated with lakes and reservoirs, the Common Buzzard with permanent crops, and the Griffon Vulture with cliffs and rocks. A weak relationship existed between Black Kites and urban settlements. There was no collinearity between the environmental variables (VIF, urban settlements = 1.098, permanent crops = 1.339, pastures = 1.450, lakes and reservoirs = 1.067, cliffs and rocks = 1.077). Arable land was removed from this analysis because it was correlated with pastures (Pearson's
correlation test, \( r = -0.594, P < 0.001 \) and generated multicolinearity (VIF > 3). The variogram of the residual inertia showed no dependence on distances because the Mantel permutation test was never significant \( (P_{\text{mean}} = 0.549, P_{\text{min}} = 0.100, P_{\text{max}} = 1.000) \).

Discussion

In this study, we provide first data on the wintering raptor community in Armenia and investigate the relationships between the environment and both the raptor community and each species during the winter in Armenia (southern Caucasus). Unfortunately, due to the sample size, we could not estimate species densities despite we collected data concerning the distances of observations. Indeed, these data could be used through some methods, such as distance sampling (Buckland et al. 1993), which use them to calculate the detectability of animals, which is very important to obtain more reliable densities estimation (Buckland et al. 1993; Buckland 2006; Marques et al. 2007). To reach the aim of this research, we used linear regression with model averaging and CCA, despite small sample sizes. The rule of thumb “one in ten” states that one predictive variable can be studied for every ten events while keeping the risk of overfitting low (Harrell et al. 1984, 1996; Peduzzi et al. 1996). Therefore, to reduce bias, we considered only models with a maximum of two predictors. However, for both species richness and diversity the null model was included in the best set of models, meaning that the uncertainty related to these response variables was not negligible. Therefore, the results concerning both the species richness and diversity should be taken with caution. Regarding CCA, Stevens (1986) found that weaker canonical correlations \( (< 0.30) \) require larger sample size \( (n > 200) \) to be detected, whereas stronger correlations \( (> 0.70) \) are evident also with smaller sample size \( (n = 50) \). Consequently, our results are reliable only for the Common Kestrel \( (n = 47) \) while for the other species they should be taken cautiously. Nonetheless, multivariate analysis is often exploratory or descriptive (Husson et al. 2010) and our results confirm general rules for habitat requirements of the species.

During the roadside census, we detected 10 species and calculated a relative abundance of 0.36 ind./km. However, considering that we collected data only in 1 year and for a short time, we do not know if these data are representative of the typical winter season. Indeed, we found a species richness lower than that reported in nearby Georgia, where 18 species are regular winter visitors (Abuladze 2013). Unfortunately, we cannot make more comparisons with other

| Table 5 | Canonical Correspondence Analysis of the relationships between species and the percentage cover of land use in the 500-m buffer around the observations |
|---------|--------------------------------------------------|
| Axis 1  | Axis 2  | Axis 3  | Axis 4  | Axis 5  |
| Eigenvalue | 0.657  | 0.140  | 0.120  | 0.090  | 0.020  |
| Proportion explained | 0.640  | 0.137  | 0.116  | 0.088  | 0.020  |
| Cumulative proportion | 0.640  | 0.776  | 0.892  | 0.980  | 1.000  |
| Permutation test |                        |         |        |        |
| F-value (\( P \)) | 6.515 (0.009) | 1.391 (0.805) | 1.184 (0.824) | 0.894 (0.794) | 0.202 (0.995) |
| Biplot scores for constraining variables |     |         |         |        |
| Urban settlements | −0.172 | −0.610 | −0.167 | 0.745 | 0.123 |
| Permanent crops | 0.294 | 0.022 | −0.917 | −0.127 | 0.237 |
| Pastures | −0.216 | −0.268 | 0.625 | −0.513 | 0.477 |
| Lakes and reservoirs | 0.987 | −0.063 | 0.101 | 0.050 | 0.100 |
| Cliffs and rocks | −0.074 | 0.771 | 0.034 | 0.463 | 0.430 |
| Species scores |          |         |         |        |
| Cinereous Vulture (AEGMON) | −0.261 | −0.009 | −0.251 | −0.849 | 0.467 |
| Griffon Vulture (GYPFULV) | −0.283 | 0.795 | 0.244 | 0.349 | 0.094 |
| Black Kite (MILMIG) | −0.267 | −0.253 | 0.279 | −0.001 | −0.050 |
| Western Marsh Harrier (CIRAER) | 3.201 | −0.103 | 0.110 | 0.128 | 0.153 |
| Hen Harrier (CIRCYA) | 0.290 | 0.049 | 0.245 | −0.491 | 0.033 |
| Common Buzzard (BUTBUT) | 1.901 | 0.190 | −0.273 | −0.054 | −0.371 |
| Long-legged Buzzard (BUTRUUF) | −0.292 | −0.128 | 0.272 | −0.136 | −0.134 |
| Eurasian Sparrowhawk (ACCNIS) | −0.383 | −1.153 | −0.659 | 1.167 | 0.360 |
| Northern Goshwak (ACCGEN) | −0.341 | −0.078 | 0.484 | −0.750 | 0.414 |
| Common Kestrel (FALTIN) | −0.207 | 0.096 | −0.466 | −0.056 | −0.057 |
neighbouring regions because of the lack of other such studies in the Caucasus during the winter. However, there are many studies in Europe and the Mediterranean Basin, and the species richness found by us (equal to 10 species) is on average respect those reported in these studies (e.g. seven to 13 species; Meunier et al. 2000; Boano and Toffoli 2002; Lucia et al. 2011; Panuccio et al. 2019a, b). Regarding the abundance, it is slightly lower than those in Europe, where 0.45–0.97 ind./km were observed during the winter (Boano and Toffoli 2002; Lucia et al. 2011; Panuccio et al. 2019a). However, our results are not surprising, because our study area was located at an average altitude of 1025 m a.s.l. and in Georgia wintering raptors usually are distributed up to 600 m, even though solitary birds can be found up to 1700 m (Abuladze et al. 2011).

Our findings showed that wintering raptors, particularly their abundance, are positively associated with the permanent crops, which in Armenia are mainly composed of vineyards and orchards (e.g. of apricots Prunus armeniaca and peaches Prunus persica). In general, other studies demonstrated that in areas of intensive agriculture, orchards and vineyards were avoided by raptors (Swolgaard et al. 2008; Pandolfino et al. 2011), likely because of the massive use of pesticides and rodenticides which are toxic to them through biomagnification in food chains (Merson et al. 1984; Blus et al. 1989; Elliott et al. 2005). However, nowadays the agricultural production in Armenia is still based on small farms (approximately 1.4 ha/farms) and extensive management systems (Avetisyan 2010). This landscape configuration may be favourable to raptors due to the habitat complexity and the resulting high diversity of prey (Santamaria et al. 2019; Serafini et al. 2019). Indeed, as a general pattern, more complex raptor communities were found in areas showing higher environmental heterogeneity (Baltag et al. 2013; Jankowiak et al. 2015a; Panuccio et al. 2019a). The use of agricultural lands could occur also because overwintering conditions are more favourable in anthropogenic landscapes than in natural habitats, due to more stable food resources and less severe weather impacts (Gil and Brumm 2014). Indeed, usually, the abundance of wintering raptors is related to mild and snowless winters (Abuladze et al. 2011; Jankowiak et al. 2015b), even though some researchers found that lower temperatures were associated with higher numbers of observed raptors, at least for some species (e.g. Common Buzzard, Rough-legged Buzzard).
Among environmental variables, we evidenced a weak negative effect of the density of rivers on the diversity of wintering raptors. In general, this should be a positive relationship, especially in arid environments (Palmer and Bennett 2006; Seymour and Simmons 2008), but in our case there are few rivers which are mainly located far from permanent crops, explaining this result. Our results showed that the community is also related to the topography, as raptors were positively associated with altitude. Particularly, we found greater abundances up to 1000–1200 m a.s.l. Again, this agrees with past research in Georgia, which has shown that the upper altitudinal limit of wintering raptor distribution is 1000 m a.s.l. (Abuladze 2013). Among species, our results showed that the Black Kite was the most abundant raptor, as found in neighbouring Georgia (Abuladze 2013). Despite most Eurasian populations migrating to spend the winter in Africa south of Sahara (Ferguson-Lees and Christie 2001), this species regularly occurs during the winter also in the Middle East (Cramp and Simmons 1980; Ferguson-Lees and Christie 2001), and in the most recent decades also in the Mediterranean Basin, likely because of the climate warming (Sara 2003; Panuccio et al. 2014; Literák et al. 2017).

The analyses showed some association between the Black Kite and urban settlements, which is consistent with past researches in the Caucasus (Abuladze 2013) and with its general habits (Cramp and Simmons 1980; Ferguson-Lees and Christie 2001). Indeed, this species is positively associated with moderate levels of human population density, mainly due to its scavenging habits and hunting opportunism (Meunier et al. 2000; De Giacomo and Guerrieri 2008; Kumar et al. 2019). Following in abundance were the Common Kestrel and the Griffon Vulture. The first had an abundance of 0.08 ind./km, similar to abundances found in the Mediterranean Basin (0.02–0.10 ind./km; Boano and Toffoli 2002; Panuccio et al. 2019a, b). However, this species is generally uncommon during winter in the Caucasus, occurring only in small numbers (Abuladze 2013). There was no apparent association with a particular habitat type, which confirms the generalist habits of this raptor (Fargallo et al. 2009; Charter et al. 2011). Griffon Vulture was the third species most abundant. It was positively associated with the amount of cliffs and rocks, these being the main used habitat (Ferguson-Lees and Christie 2001; Gavashelishvili and McGrady 2006). However, the occupancy of cliffs also during the winter season could be related to its flight strategy. Indeed, Griffon Vultures often soar on thermals (Ferguson-Lees and Christie 2001) whose strength and regularity are positively related to the amount of sunlight and terrain ruggedness (Pennycuick 2008). Thus, the presence of cliffs, especially those that are south-facing, can produce regular thermal lifts, which ensure better flight conditions for the species (Gavashelishvili and McGrady 2006; Miller et al. 2017). Our analyses allow us to draw some conclusions about the habitat use also of other species. Unsurprisingly, the occurrence of Western Marsh Harrier is related to lakes and reservoirs, a rule for the species year-round (Cramp and Simmons 1980; Ferguson-Lees and Christie 2001), also in western Asia (Abuladze 2013; Al-Sheikhly and Al-Azawi 2019). Common Buzzards are mainly associated with permanent crops. Similarly, in Eastern Europe and Crete the species uses permanent crops (e.g. olive Olea europea groves) and other agricultural lands during the winter ( Nikolov et al. 2006; Tzortzakaki et al. 2012; Baltag et al. 2013; Panuccio et al. 2019a), even if meadows are the main habitat type used for hunting in some places (Wuczyński 2005; Tapia et al. 2008; Wikar et al. 2008). Finally, the Eurasian Sparrowhawk is related to urban settlements. The use of built-up areas during winter, especially with large gardens and parks, is common for this species, which are favoured because of high prey density found in this environment in this season (Chamberlain et al. 2009; Schütz and Schulze 2018).

In conclusion, the wintering raptor community in Armenia at high altitude was poor and, as a general pattern, is related mainly to permanent crops, maybe because of their heterogeneity, which in turn support higher prey density during the winter. The most abundant species is the Black Kite, which regularly spends the winter in the Caucasus and is related to urban settlements, followed by the Common Kestrel and the Griffon Vulture. From a conservation perspective, if land use changes will happen in the next decades in Armenia, it should be kept in mind that the habitat heterogeneity could be the key to support a diversified community of raptors during the winter. However, nowadays the agricultural production in Armenia is still based on extensive management systems, even though in the next future plantations will be irrigated and mechanical pruning and harvest will occur, especially in vineyards (Avetisyan 2010). Anyway, some evidence shows that the irrigation of crops could be favourable for raptor conservation in low-intensity farming systems (Eisenman 1971; Ursúa et al. 2005), even if the intensive irrigation, as well as heavy intensification of agricultural practices in general, is detrimental also for these birds (Bird et al. 1996; Tella and Forero 2000; De Frutos et al. 2015).
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Availability of data and material The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest.

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