Network topology of stable isotope interactions in a sub-arctic raptor guild

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Oecologia In Press

Abstract:

Predation is an ecologically important process, and intra-guild interactions may substantially influence the ecological effects of predator species. Despite a rapid expansion in the use of mathematical graph theory to describe trophic relations, network approaches have rarely been used to study interactions within predator assemblages. Assemblages of diurnal raptors are subject to substantial intra and interspecific competition. Here we used the novel approach of applying analyses based on network topology to species-specific data on the stable isotopes ^{13}C and ^{15}N in feathers to evaluate patterns of relative resource utilization within a guild of diurnal raptors in northern Sweden. Our guild consisted of the golden eagle (*Aquila chrysaetos*), the gyrfalcon (*Falco rusticolus*), the peregrine falcon (*Falco peregrinus*) and the rough-legged buzzard (*Buteo lagopus*). We found a modular trophic interaction structure within the guild, but the interactions were less nested than expected by chance. These results suggest low redundancy and hence a strong ecological importance of individual species. Our data also suggested that species were less connected through intra-guild interactions than expected by chance. We interpret our results as a convergence on specific isotope niches, and that body size and different hunting behaviour may mediate competition within these niches. We finally highlight that generalist predators could be ecologically important by linking specialist predator species with disparate dietary niches.

Introduction

Predation is a key component in most ecological systems, imposing both direct and indirect effects on ecosystem properties (Taylor 1984; Terborgh et al. 1999). Interactions between functionally similar predators may influence their ecological roles (Sih et al. 1998). The ecological consequences of such interactions are determined by the relative ecological attributes of co-existing species (Dalerum et al. 2012). Therefore, the structure of predator assemblages, as well as the species interactions within such assemblages, may have pivotal influences on the overall effects of predation in any given ecosystem (Sih et al. 1998; Woodroffe and Ginsberg 2005; Dalerum 2013).

An emerging interest in community ecology has led to the adaptation of mathematical graph theory to describe trophic relations among species (Proulx et al. 2005). However, despite its applicability to predation processes, topological approaches to study trophic interactions within predator assemblages have been surprisingly neglected (Miranda et al. 2013). In an ecological context, a trophic network typically consists of two sets of discrete nodes that are connected through links representing resource use (Elton 1927), where the nodes usually represent species or other recognizable taxonomic units, although exceptions exists (e.g., Miranda et al. 2014). Characterizations of trophic network topology allow for evaluations of interspecific patterns in resource use (Sugihara 1984), where nested and modular patterns may be particularly relevant for ecosystem properties (May 1973, Bascompte et al. 2003; Newman 2006; Thébault and Fontaine 2010; Stouffer and Bascompte 2011). Nested patterns emerge when the resources used by specialist consumers are a subset of the resources used by generalist ones (Bascompte et al. 2003). In nested patterns of resource use, there is thus a large redundancy that may improve the stability of ecosystem dynamics (Holling 1973). A modular pattern is characterized by delimited sub-communities of consumers and resources, with more frequent and stronger interactions between organisms within than between sub-communities (May 1973; Prado and Lewinsohn 2004). Modular patterns may be ecologically important by delimiting the impacts of perturbations to specific modules, so that they may not permeate through the entire ecosystem (Stouffer and Bascompte 2011).

However, much of our theoretical understanding of network topology comes from networks that quantify interactions among only one set of nodes, i.e. unipartite networks. It may therefore be fruitful to also re-project bipartite networks into unipartite ones (Newman 2001; Opsahl 2009), which then will link species on the same trophic level through interactions quantified from shared resources (Padrón et al. 2011). Unipartite projections of trophic interactions can hold useful information regarding intraguild processes, such as competition and facilitation among species (Miranda et al. 2013), as well as ecosystem properties of consumer guilds (Dunne et al. 2002; Jordán 2009). They may also aid in identifying ecologically important species (Jordán et al. 2006) and to identify species most likely to be influenced by ecosystem perturbations such as biological invasions (Carvalheiro et al. 2008). The relative importance of individual species can be quantified through centrality indices, which for trophic networks describe the number of other species with which a species share resources (Estrada 2007).

Analysis of naturally occurring stable isotopes has become well established as a tool for investigating consumer resource use (Dalerum and Angerbjörn 2005; Martínez del Rio et al. 2009). However, topological approaches have rarely been applied to stable isotope data (but see Miranda et al. 2014). This is unfortunate, because isotope data contain information

about resources assimilated over time. They can therefore provide supplementary information to more direct methods of resource use, and hence provide a more complete evaluation of the resource use among and within consumer assemblages.

Raptor assemblages are subject to substantial intra and interspecific competition, where local environmental factors often determine the importance of competition in any given raptor community (Jaksić and Braker 1983). Raptors can have significant ecological effects and function as efficient umbrella species for biodiversity conservation (Sergio et al. 2006). In this study, we used stable isotopes of carbon and nitrogen in the feathers of four species of diurnal raptors in northern Sweden, the golden eagle (*Aquila chrysaetos*), the rough-legged buzzard (*Buteo lagopus*), the gyrfalcon (*Falco rusticolus*), and the peregrine falcon (*Falco peregrinus*), to evaluate patterns of relative resource utilization within and among these sympatric predators in a sub-arctic environment. In particular, we used topological approaches to identify if there was any evidence for nested and compartmental community structures, and to evaluate if the patterns of intra-guild interactions suggested inter or intra-specific competition or facilitation.

Methods

Study area and sample collection

Feather samples were collected while conducting routine monitoring of 39 golden eagle nests, 14 rough-legged buzzard nests, 13 gyrfalcon nests, and 3 peregrine falcon nests. All nests were in the foothills of the Fennoscandian mountain range in the two northernmost counties in Sweden (Norrbotten and Västerbotten). We collected a total of 111 moulted flight feathers, 37 form adult and 26 from juvenile golden eagles, 12 from adult and 8 from juvenile rough legged-buzzards, 19 from juvenile gyrfalcons and 9 from juvenile peregrine falcons. The nests were visited during June and July (Nyström et al. 2005; Nyström et al. 2006; Hellström et al. 2014). Hence, the isotope values in feathers from juvenile birds reflect the diet of the current spring and summer. Moulting patterns in adult raptors is varied, with both eagles and buzzards showing serial moult, were a section of the primaries are at any given time, whereas large falcons tends to replace most flight feathers annually (Edelstam 1984). Regardless of moult pattern, however, moult in all four species is generally carried out during spring – early autumn, and the growth period for a single quill is 1-2 months (Jollie 1947; Edelstam 1984; Clark 1999). Therefore, the feathers from adult birds likely reflect the diet of spring and summer from one (the two falcon species) to up to three (golden eagle and buzzard) years prior to the year of collection. Samples were collected in 1998 – 2003 for golden eagles, 2004 for rough-legged buzzards, 2002 and 2003 for gyrfalcons, and 2003 for peregrine falcons. Temporal variation between years of collection did not influence the relative differences in isotope values among the raptor species (Manova, $F_{2,98} = 0.06$, $P = 0.19$). In addition to the raptor feathers, we compiled available data on isotope values from potential prey species (Table 1). These are not reported as a comprehensive range of potential prey or a detailed account of the available isotope niches, but are presented to illustrate the isotope variation that caused the observed interaction patterns.

The Fennoscandian mountain range in northern Sweden is characterized by tree-less or willow-based sub-arctic mountain tundra above approximately 800 m altitude, and boreal forest dominated by Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) at lower altitudes. Key food sources for raptors are carrion of moose (*Alces alces*) and semi-

domesticated reindeer (*Rangifer tarandus*), as well as potential prey species such as mountain hares (*Lepus timidus*), Norwegian lemming (*Lemmus lemmus*), microtine rodents (*Microtus agrestis*, *Myodus rufocanus*, and *Myodes glareolus*), two species of grouse (*Lagopus lagopus* and *Lagopus muta*), and various species of migratory birds.

Sample treatment and stable isotope analyses

We rinsed feathers by sonicating them in a chloroform/methanol/water (1:2:1) solution to remove surface attached lipids and contaminants, and after air drying we clipped 0.1 – 0.8 g into tin capsules for analyses. We analyzed $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios on a Carlo Erba elemental analyzer (E1108 CHNS-O) connected to a Fison Optima isotope ratio mass spectrometer, with a standard deviation of <0.1%. Isotope values are presented as dX values, which represent the proportional deviation in parts per thousand (‰) from a standard: $X = 1000$ x $(R_{sample}/R_{standard})-1$, where X is either $\delta^{13}C$ or $\delta^{15}N$ and R is either 13C/12C or 15N/14N, respectively. The accepted standard for carbon is Pee Dee Belemnite (PDB) and the standard for nitrogen is air.

Data analyses

To describe the structure of isotope relationships between the different study species and age classes, we adapted network tools derived from graph theory (Miranda et al. 2013). We conducted our analyses on separate age classes partly since certain prey may have been favoured to bring back to the nests (e.g., Lindström 1994; Catry et al. 2016), and partly because the isotopes in adult and juvenile feather reflected different time periods. We first generated a bipartite network for each element, in which the consumer nodes represented the species and age class categories and the resource nodes a categorized representation of respective $\delta^{13}C$ and $\delta^{15}N$ values (Miranda et al. 2014). We set all isotope categories within each element to be of equal width. We defined the isotope width of each isotope category as the average standard deviation of isotope values within species and age class groups, which was 0.4 for $\delta^{13}C$ and 0.78 for $\delta^{15}N$. We weighted the networks by the number of individuals that contributed to a specific isotope class. Secondly, we projected the weighted bipartite networks into weighted unipartite networks to further describe the structure of interactions between the different consumer groups. In these projected networks, shared utilization of an isotope category between two consumer groups was represented as a link, which was weighted according to the number of individuals that contributed to the link (i.e. shared the isotope category with another group). We used raw isotope data without attempting to correct for isotopic fractionation in the analyses (Table 1).

We used the QuaBiMo algorithm to determine the degree of modularity (Q) in the bipartite networks (Dormann and Strauss, 2013). This algorithm adapts a simulated annealing-Monte Carlo procedure to identify the best aggregation of links into modules (Danon et al. 2005). Following Dormann and Strauss (2013), we set the number of swaps to 10^6. The modularity index Q ranges from 0, indicating that links within modules are not higher than expected by chance, to a maximum value of 1 when modules are completely discretely delimited. We have presented the identified modules in interaction matrices, which provide a visual representation of the identified modules (Dormann and Strauss 2013).

We used the weighted-interaction nestedness (WIN) index to quantify the degree of nestedness in the bipartite networks (Galeano et al. 2008). This value is calculated by

ordering the rows of the interaction matrix from top to bottom and columns from left to right, in ascending order according to the number of links. The WIN is then calculated as the mean weighted Manhattan distance from each of the matrix cells containing a link to the cell corresponding to the intersection of the row and columns with the lowest link number (see Galeano et al. 2008 for detailed descriptions of calculations). For ease of interpretation, however, we have presented the nestedness values as the weighted nestedness estimator (WINE), which ranges from 0 which represents a completely random interaction structure to 1, which represents a maximally nested structure (Galeano et al. 2008).

In the unipartite projections, we calculated a weighted degree centrality index for each species and age class (Freeman 1979). This index quantified the number of other species and age classes that shared isotope values weighted by the number of individuals contributing to each link. This value thus describes how many other raptor groups each group share its isotope values with. We opted for this local index since our network was very small. Therefore, other centrality indices that better quantify centrality through indirect links between regions in larger networks were not directly relevant (Jordán et al. 2006). In addition to calculating degree centrality for each of the species and age-class groups, we also calculated the average degree centrality across species and age classes as a representation of the degree of centrality in each unipartite network. Such network scale metrics can provide information of the relative patterns of resource partitioning within consumer guilds.

To evaluate if the values of modularity, nestedness and centrality deviated from random expectations, we compared the observed values to those obtained from 1000 random matrices. The random matrices were constrained to retain marginal totals (abundances) from the original matrix, to control for unequal numbers of sampled animals across species and age classes. Each random bipartite matrix was also projected into a unipartite matrix, to enable comparisons of centrality measure to random expectations. We converted each observed metric to a z-score by subtracting the mean and dividing by the standard deviation of each respective random distribution, to allow for a formal evaluation of departure from random expectations in each observed index value. To enable comparisons between metrics derived for $\delta^{13}C$ and $\delta^{15}N$, we subtracted the values calculated from the random matrices from each observed value (Manly 1997), and used these deviations from random expectations to compare compartmentalization, nestedness and centrality between the $\delta^{13}C$ and $\delta^{15}N$ networks using two sample permutation tests.

Statistical analyses were conducted in the package R version 2.15.1 for Mac and Linux (http://www.r-project.org) using the user contributed packages bipartite (Dormann et al. 2008), coin (Hothorn et al. 2008) and network (Butts 2008).

Results

The interaction patterns of both the $\delta^{13}C$ and $\delta^{15}N$ bipartite networks were less nested but more modular than random expectations (Table 2). The $\delta^{13}C$ interaction patterns had both lower degree of modularity ($Z = -39.27$, $P < 0.001$) and were less nested ($Z = -18.65$, $P < 0.001$) than the $\delta^{15}N$ interactions (Fig. 1a,b). For $\delta^{13}C$, adult and juvenile rough-legged buzzards formed a module containing values relatively depleted in ^{13}C, adult and juvenile golden eagles formed a module together with juvenile peregrine falcons containing intermediate $\delta^{13}C$ values, and gyrfalcons formed an isolated module containing values

relatively enriched in ^{13}C (Fig. 1c). For δ^{15}N, adult golden eagles and juvenile peregrine falcons formed a module containing values relatively enriched in ^{15}N, juvenile golden eagles formed a module together with adult and juvenile rough-legged buzzards containing intermediate δ^{15}N values, and gyrfalcon again formed an isolated module containing values relatively depleted in ^{15}N (Fig. 1d).

The unipartite projections of both the δ^{13}C and δ^{15}N bipartite relationships showed less degree centrality than random expectations (Fig. 2a,b, Table 2), but the δ^{13}C interactions showed higher degree centrality than the δ^{15}N ones ($Z = 20.37$, $P < 0.001$). Similar patterns were found for all the species, which had lower degree centrality than random expectations (Table 2) and consistently higher degree centrality for δ^{13}C than for δ^{15}N interactions (adult golden eagle: $Z = 35.70$, $P < 0.001$; juvenile golden eagle: $Z = 35.92$, $P < 0.001$; adult rough legged buzzard: $Z = 9.67$, $P < 0.001$, juvenile rough-legged buzzard: $Z = 23.31$, $P < 0.001$; juvenile gyrfalcon $Z = 6.96$, $P < 0.001$, juvenile peregrine falcon $Z = 34.22$, $P < 0.001$). For both the δ^{13}C and the δ^{15}N interactions, golden eagles had the highest degree centrality (Table 2) and gyrfalcon and peregrine falcon shared few isotope values with the other species, particularly for δ^{15}N (Fig. 2b).

Discussion

We observed significant modular structures of the isotope interactions within the raptor guild, and we similarly observed less nested isotope interaction patterns than random expectations. Modular structures have previously been linked to an increased stability of the ecosystem process of concern, because any effects of perturbations likely will be restricted within isolated modules (Prado and Lewinsohn 2004; Stouffer and Bascompte 2011). However, the lack of nested patterns suggests little redundancy across modules. Such lack of redundancy has previously been suggested for top predators (Woodroffe and Ginsberg 2005), and highlights that any ecosystem effects of raptor predation in the sub-arctic areas of northern Sweden may be fragile and that the loss of individual species may highly influence ecosystem dynamics.

If re-projected into unipartite graphs, interactions quantified both through δ^{13}C and through δ^{15}N yielded networks with lower degree centrality than expected by chance. These results imply that the raptor species were separated in their isotope values more than what would have been the case if they had randomly distributed across carbon and nitrogen isotope space. We suggest that these observed patterns may reflect competition-mediated resource partitioning (sensu Schoener 1974). Of the four species, the golden eagle was the most connected, both in terms of interactions through δ^{13}C and δ^{15}N. This result agrees with the relative predation strategies between the four species, where golden eagles have a much broader dietary niche (e.g., Tjernberg 1981; Nyström et al. 2006) compared to both rough-legged buzzards (Hellström et al. 2014) and the two falcon species (Mearns 1983; Rosenfield et al. 1995; Nyström et al. 2005). We suggest that these results points to a potential role for generalist predators to function as ecological links between specialist predators with disparate diets. Such ecological homogenization could have important consequences for both predator and prey populations, and we highlight that while specialist predators may be ecologically important by directly influencing their prey populations (Anderson and Erlinge 1977), the ecological effects of generalist predators may partly be related to indirect effects caused by linking otherwise un-connected ecological components (Abrams 1983; Martín-González et al. 2009).

For our raptor guild, we suggest that the modular patterns reflect substantial dietary overlap within modules (e.g., between rough-legged buzzards and golden eagles and between golden eagles and peregrine falcons), but that the low centrality values nevertheless suggest a significant competition-mediated resource partitioning. We suggest that the substantial size differences, as well as differences in hunting behaviour, may sustain these modular structures in the face of potential inter-specific competition (Brown and Wilson 1956). For both the $\delta^{13}C$ and the $\delta^{15}N$, gyrfalcon formed a separate module, which illustrates the contrasting predator strategies of this species, which almost exclusively prey on ptarmigan (Nyström et al. 2005).

We found lower structuring of interactions in $\delta^{13}C$ compared to $\delta^{15}N$ networks. In terrestrial ecosystems, variation in $\delta^{13}C$ is usually mediated by contrasts between plants with C3 and C4 photosynthesis, and by input from marine vs. terrestrial carbon, whereas variation in $\delta^{15}N$ is more complex (Peterson and Fry 1987). In northern Sweden, terrestrial ecosystems are largely dominated by plants of the C3 photosynthetic pathway (Still and Berry 2003), and the low $\delta^{13}C$ in the raptor feathers points to a limited influence of prey that are connected to marine resources (e.g., Chisholm et al. 1982). We suggest that our observation of higher structuring in $\delta^{15}N$ is a reflection of properties of the terrestrial origin of the food chains, of which raptors are a part, where processes such a nitrogen fixation and the trophic position of prey may influence the relative isotope niches exhibited by the individual species

To conclude, our approach to analyse stable isotope data using network topology suggested a compartmentalized trophic interaction structure among large Swedish raptors, but we found that species were less connected through intra-guild interactions than suggested by chance. We interpret these results as an indication of convergence on specific isotope niches, and that body size and different hunting behaviour mediates competition within these niches. We further found no nested interaction structures, suggesting low redundancy and a potentially high ecological importance of individual species. Finally, we found that the most generalist species had the highest centrality value, which exemplifies that generalist predators may be critically important by linking otherwise separated ecological components.

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Table 1. Raw isotope data from feathers of northern Swedish raptors as well as representative values of $\delta^{13}C$ and $\delta^{15}N$ for potential prey items.

Common name	Latin name	n	C	N	Area	Reference
Golden eagle, ad	*Aquila chrysaetos*	37	−22.5 ± 0.55	7.80 ± 0.73	Northern Sweden	This study
Golden eagle, juv	*Aquila chrysaetos*	26	−22.6 ± 0.55	5.06 ± 1.13	Northern Sweden	This study
Rough-legged buzzard, ad	*Buteo lagopus*	12	−23.2 ± 0.48	5.91 ± 0.89	Northern Sweden	This study
Rough-legged buzzard, juv	*Buteo lagopus*	8	−23.8 ± 0.15	3.52 ± 1.02	Northern Sweden	This study
Peregrine falcon, juv	*Falco peregrinus*	9	−22.7 ± 0.29	8.12 ± 0.49	Northern Sweden	This study
Gyrfalcon, juv	*Falco rusticolus*	19	−21.4 ± 0.36	3.52 ± 1.02	Northern Sweden	This study
Prey reference values[a]						
Moose	*Alces alces*	59	−24.7 ± 0.51	1.05 ± 0.79	Alaska	Adams et al. 2010
Moose	*Alces alces*	7	−25.6 ± 0.5	3.1 ± 0.83	Saskatchewan	Urton and Hobson 2005
Reindeer	*Rangufer tarandus*	21	-22.22±0.17	2.67±0.51	Central Norway	Reitan 2013
Mountian hare	*Lepus timidus*	22	-26.09±0.94	3.21±1.31	Central Norway	Reitan 2013
Scandinavian lemming	*Lemmus lemmus*	5	−29.0 ± 1.3	1.4 ± 1.0	Varanger peninsula	Ehrich et al. 2011
Grey-sided vole	*Myodes rufocanus*	4	−27.2 ± 11	0.3 ± 1.7	Varanger peninsula	Ehrich et al. 2011
Galliformes	*Lagopus lagopus Tetrao urogallus*	22	-23.77±0.57	0.61±0.88	Central Norway	Reitan 2013
Small passerines	*Calcarius lapponicus, Plectrophenax nivalis, Carduelis flammea*	3	−26.1 ± 0.8	5.1 ± 1.9	Alaska	Weiser and Powell 2011
Greylag goose	*Anser anser*	12	−26.4 ± 0.35	8.35 ± 0.55	Denmark	Fox et al. 2009
Mallard	*Anas platyrhynchos*	102	−23.3 ± 3.64	9.47 ± 2.59	Central USA	Szymanski et al. 2010
Shorebirds	*Phalaropus lobatus, Pluvialis dominica*	2	−28.1 ± 2.1	7.4 ± 0.7	Alaska	Weiser and Powell 2011

[a] Prey reference values are from muscle tissue except for Greylag goose, which values are from flight feathers.

Table 2. Observed values of compartmentalization, nestedness, and degree centrality in bipartite (compartmentalization and nestedness) and unipartite (degree centrality) network representations of $\delta^{13}C$ and $\delta^{15}N$ in feathers from juvenile and adult feathers from golden eagle (GE), rough-legged buzzard (RLB), gyrfalcon(GF) and peregrine falcon (PF), as well as z-scores calculated from 1000 random matrices and associated p-values. The network values for centrality were calculated as the average of the individual species values

|	$\delta^{13}C$			$\delta^{15}N$		
	Observed value	Z-score	p	Observed value	Z-score	p
Modularity	0.38	9.20	<0.001	0.49	12.83	<0.001
Nestedness	0.04	-1.97	0.024	-3.86×10^{-4}	-3.34	<0.001
Degree centrality	52.50	-6.61	<0.001	38	-8.84	<0.001
Juvenile GE	81	-3.57	<0.001	56	-5.98	<0.001
Adult GE	116	-3.67	<0.001	82	-6.01	<0.001
Juvenile RLB	24	-3.87	<0.001	19	-3.88	<0.001
Adult RLB	37	-4.31	<0.001	33	-4.55	<0.001
Juvenile GF	27	-10.22	<0.001	21	-9.18	<0.001
Juvenile PF	30	-3.16	<0.001	21	-5.01	<0.001
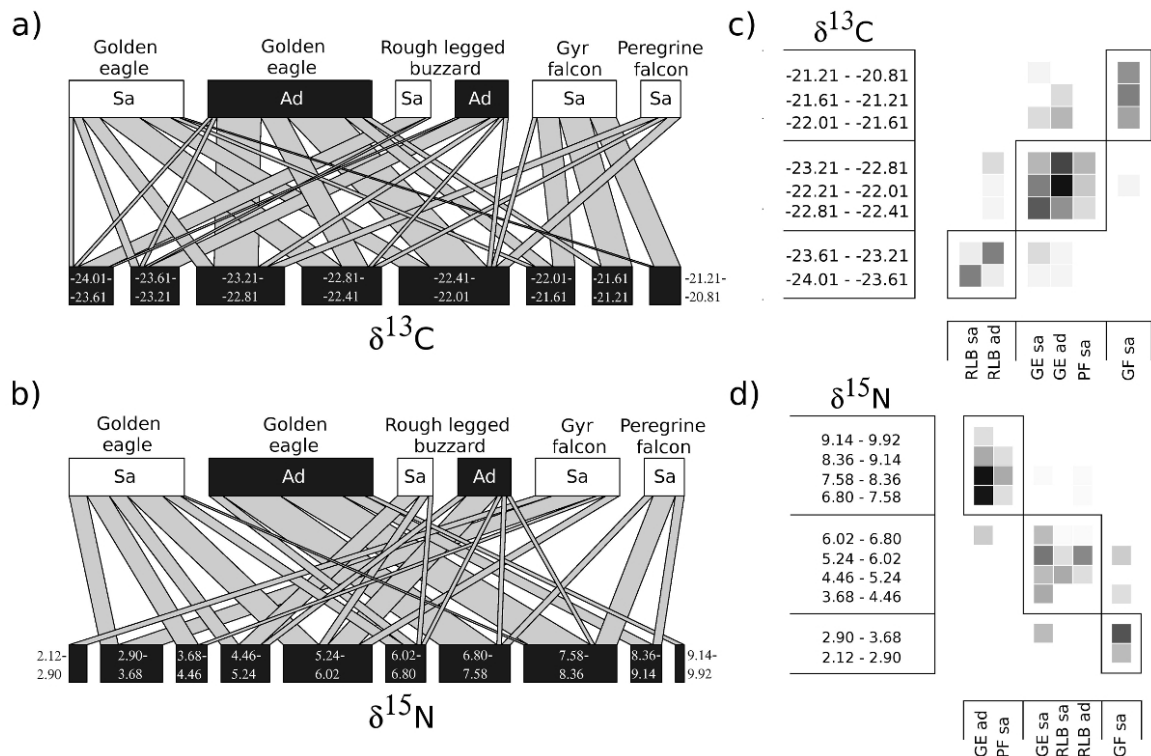
Figure 1. Bipartite network representations of the isotope composition in feathers of adult and juvenile golden eagles and rough-legged buzzards, and juvenile gyrfalcons and peregrine falcons for a) δ13C and b) δ15N, as well as raptor isotope interaction matrices for c) δ13C and d) δ15N. The width of the isotope categories was determined as the average standard deviation of the species-specific standard deviations for each isotope. The width of each link in the bipartite graphs reflects relative interaction frequency, i.e. the number of individuals it contains. The interaction matrices delineates modules found in the bipartite networks, and are coded so that darker cell values indicate higher numbers of interactions.
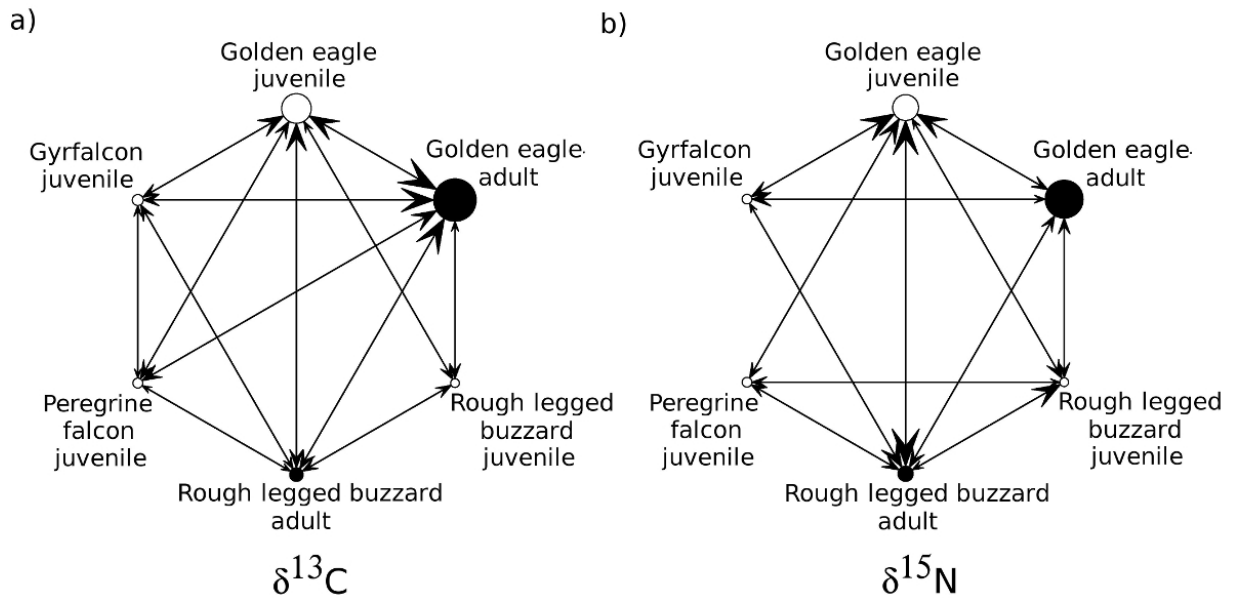
Figure 2. Unipartite projections of bipartite raptor – isotope networks, describing the relationships between species and age classes by their respective δ^{13}C (a) and δ^{15}N (b) values. Each node represents a raptor species and age class, and each line represents the occurrence of a shared range of isotope values between two nodes. Node sizes are coded by the relative degree centrality, which describes the weighted number of connections for a specific node, and hence how connected that specific species and age class is in each isotope network. The arrows are coded by the proportion of incoming links to each specific node, and hence provide information on which other species and age classes that each node shares its isotope values with.