Modularity of trophic network is driven by phylogeny and migration in a steppe ecosystem

Abstract

Evidence is mounting that the structures of trophic networks are governed by migratory movements of interacting species and also by their phylogenetic relationships. Using the largest available trophic network of a large steppe ecosystem, we tested that steppe trophic networks including migratory species are associated with (i) migratory strategy and (ii) phylogenetic relatedness of interacting species: (1) whole graph-level metrics, estimated as modularity, and (2) species-level network metrics, measured as node degree (number of interacting partners), and centrality metrics. We found that (1) a substantial number of links were established by migrant taxa; (2) the phylogenetic signal in network structure was moderate for both consumer and prey nodes; (3) both consumer and prey phylogenies affected modularity, which was modulated by migration strategy; and (4) all species-level graph properties significantly differed between networks including and excluding migratory taxa. In sum, here we show that the structure of steppe trophic networks is primarily governed by migratory strategies and to a lesser extent, by phylogenetic relatedness, using the largest available food web representative for steppe ecology and migration biology.

Keywords: Hortobágy, phylogenetic controll, ecological interaction, graph property
**Introduction**

Organisms interact with each other to form highly structured complex networks, leading to ecological communities (Bascompte et al., 2003; Olesen et al., 2007; Thébault & Fontaine, 2010, Poisot et al. 2016). The architecture of these webs ranges from unnested to nested patterns of links, the analysis of which is important for the understanding of ecological, evolutionary and coevolutionary processes (e.g. Lewinsohn et al., 2006; Dormann et al. 2017, Pellissier et al. 2017, Tylianakis & Morris 2017).

Specifically, numerous investigations of trophic network structure have detected that topology, strength and type of trophic interactions conform to a limited number of defining rules. For example, food webs have been shown to be key determinants of ecosystem functionality as their topology defines energetic processes and underpins key processes including network resilience (Loreau & Behera, 1999, Kéfi et al. 2015).

Trophic networks among species are not governed solely by species co-occurrences, but also by phylogenetic relatedness of interacting species. Therefore, phylogenetic signal inherent in food webs suggests that evolution plays a key role in determining community architecture and thus could deepen our understanding of the underlying mechanisms. (Peralta 2016). Consequently, the investigation of such networks requires the consideration of the phylogenetic histories of both sets of participants in an ecological interaction (Hadfield et al. 2013, Rafferty & Ives 2013). Theory predicts that closely related species are ecologically more similar to each other than expected based solely on the timing of their phylogenetic divergence, as a result of phylogenetic niche conservatism (Peterson et al. 1999). Indeed, niche conservatism has been demonstrated in numerous plants and animals, several ecological and life-history traits as well as network metrics (Freckleton et al. 2002; Qian & Ricklefs 2004).

Recently, investigations of the properties of time-aggregated networks revealed that temporal dynamics should be considered in several ecological and evolutionary questions and consistently concluded that network analyses ignoring or not adequately accounting for temporal patterns might provide biased results (Blonder et al. 2012).

An important aspect of temporal changes in the composition of trophic networks is provided by the presence and absence of migratory animals. Indeed, Bauer & Hoye (2014) showed that migratory species forage and are preyed upon throughout their journeys, thereby establishing trophic interactions with other migrants and resident communities. Specifically, migrant and resident species are fundamentally different by the timing of their interactions, governing
relationships between migrant abundance and primary production as well as the stability of trophic networks. Thus, presence and absence of migrants might substantially change the structure of food webs.

One of the primary ecological functionalities of grassland ecosystems include providing migratory hotspots for billions of migratory birds and insects, especially in steppe ecosystems with considerable amounts of wetland habitats (Sanderson et al. 2006, Zwarts et al. 2009). One of the key migratory hotspots for birds migrating along African-Palearctic flyways is represented by the Hortobágy steppe in East-Hungary, where up to 500,000 birds migrate on an annual basis, which is considered as the westermost outpost of the Eurasian steppe zone (Chibilyev 2002, Ecsedi et al. 2004).

Up to now, no published datasets are available which include information on trophic networks accounting for migration strategy and phylogeny. In our study we investigated the role of migration strategy and evolutionary relatedness on the temporal development of trophic network structure using the largest dataset of trophic links in a representative steppe ecosystem.

To do so, we hypothesized that network properties, which have been shown to be of relevance for characterising trophic networks including migratory species, are associated with (i) migratory strategy and (ii) phylogenetic relatedness of interacting species. The phylogenetic dependence was estimated applying (1) whole-level metrics, estimated as modularity, which has been shown to be present in virtually all ecological networks analyzed so far (Dormann et al. 2017) and which is often related to phylogenetic patterns of ecological networks (Lewinsohn et al. 2006); (2) species-level network metrics, measured as node degree (number of interacting partners), and centrality metrics; Guimera & Amaral 2005, Pavlopoulos et al. 2011).

To test these relationships, we calculated all of these network metrics for the Hortobágy network on a weekly scale and applied information theoretic approach to retrieve the relative importance of migration and phylogeny in governing food web topology.

Methods

Data collection

We compiled a trophic network for animals and plants totaling 535 taxa which reproduce, migrate or winter in Hortobágy region of Hungary. The Hortobágy covering 800 km2 is the largest alkali steppe complex of Europe, the westermost occurrence of the Eurasian steppe and is recognised as one of the steppe regions where ecosystem processes have remained relatively undisturbed, thus representative for the whole region in terms of ecological functionality.
Furthermore, the region is acknowledged as the most important stopover site and wintering area along the Baltic-Hungarian Flyway harbouring significant populations of European waterbirds, waders, raptors and passerines (Ecsedi et al 2004, Végvári et al. 2010, Mingozzi et al. 2013). Our dataset contains information on 53 bird species, which occur only as migrant in the study area.

To assemble the trophic web, we used all known direct trophic interactions, i.e. consumer-prey relatedness among co-occurring species based on expert knowledge derived from literature data and our own observations in the Hortobágy steppe region (Mahunka 1981, Szukó-Lacza 1981, Ecsedi et al 2004). These works cover four decades and provide replicated estimates on presence-absence data with representative spatial coverage of the Hortobágy steppe. Thus, our network included all species which co-occur during reproduction, migration or wintering in the Hortobágy steppe (see Ecsedi et al. 2004 and Végvári et al. 2010 for sampling methodology and taxon list, see Appendix 1 for species list and migration types (migratory or resident). Due to limited information, our dataset excludes parasites, amphipods and isopods. The trophic network is time-integrated on a weekly time-scale, thus providing 52 networks representing all weeks of the year (Kéfi et al. 2015).

We constructed species-by-species matrices for trophic interactions for each week of the year, coded as 0 or 1 (species i feeds on species j or not, which are evidently unidirectional effects of species i on species j (Appendix 1). The final matrix of these interactions yields the most comprehensive description of trophic interactions among all 535 species of the Eurasian steppe ecosystem. The dataset is available in an editable, annotatable, and shareable cloud-based network visualization software (available online at the Dryad Data Repository - https://datadryad.org/)

**Network parameters**

For each weekly aggregated network, we calculated several network characteristics, capturing different aspects of the biological significance of each species to the food web (González et al 2010, Kéfi et al. 2015).

1. We quantified network structure by identifying modules, defined as strongly interconnected groups of nodes which are only weakly linked to other highly connected groups (Guimera & Amaral 2005). Modularity is a metric of the proportion of edges located within modules minus the the expected value in a similarly structured random network with random links, ranging between 0.0 and 1.0, where 1.0 is assigned to a perfectly modular network, i.e. zero stands for no subgroups, whereas 1 indicates totally separated subgroups.
(2) We further calculated weekly-averaged mean values of species-level network metrics, representatively describing food webs:

(a) node degree, calculated as the sum of incoming and outgoing links, including all preys and predators of a given taxon.

(b) Centrality indices, that characterize the importance of single nodes or links in the network (Paulau et al. 2015): (i) closeness centrality, defined as the inverse of the mean shortest path length from a species to all the other species in the network, which indicates important nodes that can communicate quickly with other nodes of the network (Pavlopoulos et al. 2011); (ii) betweenness centrality, calculated as the extent to which a focal species lies on the shortest paths between two other species, which shows that nodes which are intermediate between neighbors rank higher. Without these nodes, two neighbors would not be able to be connected to each other (Pavlopoulos et al. 2011). Thus, betweenness centrality shows important nodes that lie on a high proportion of paths between other nodes in the network (Freeman 1979); finally, (iii) alpha centrality, which is an adaptation of eigenvector centrality measuring the species’ importance based on whether it has connections to other species that are themselves important; alpha centrality enhances this process by allowing nodes to have external sources of influence.

Statistical analyses

Non-randomness

The above graph metrics were also calculated for 10000 random networks with the same overall connectivity as the empirical network to assess whether the empirical food web statistically differed from random networks (Guimerà et al. 2004, Kéfi et al. 2015). If a specific measure from the empirical network lay outside mean ± SD of that measure in the random network, we assumed it statistically differed (Bornatowski et al. 2017).

Phylogeny

In the absence of a complete molecular phylogeny for all species included within our trophic network, each species was classified into a nested taxonomic hierarchy including family, order, class and phylum, based on the comprehensive systematic classification from the Tree of Life (Letunic & Bork 2006). To quantify the phylogenetic signal of networks, we fitted a generalized linear mixed model (Peralta 2016), using connection type (connected or unconnected links defined on the complete set of studied species) as binary response, and the taxonomic class of consumer (belonging to N = 115 families) and prey species (classified into N = 142 families), both employed as a hierarchically nested random factor, defined as kingdom/phylum/class/order/family, applying
binomial logit link. In the next step, the degree of phylogenetic dependence was measured as the variance explained by the nested random terms. This metric of taxonomic heritability is considered as an estimate of the phylogenetic signal in the data. (Nakagawa & Schielzeth 2013; Kéfi et al. 2015).

**Effects of migration and phylogeny network topology**

To estimate the effects of migratory strategy and phylogenetic relatedness on present network topology, we formulated linear models for each graph metric using the degree of phylogenetic relatedness among consumer and prey species (calculated as the variance of the nested random term defined in Phylogeny subsection), week and migration strategy (separated for strategies and pooled) as fixed predictors. The importance of these predictors was evaluated applying AIC-based model selection within the information-theoretic framework (Kenneth et al. 2002).

All analyses were run with R 3.1.0, including the “igraph” package for calculating network properties (Csárdi & Nepusz 2006).

**Results**

**Distribution and non-randomness of network properties**

Out of the 289962 edges of the trophic network of Hortobágy steppe ecosystem, 23867 (8.2%) included at least one node represented by a migrant species. While migrant nodes were constituted by 247 genera, resident links were generated by 467 genera (Appendix 1-2, Fig 1). Consumer species of migrant nodes included 34 genera (all birds), which amounted to 12.1% that of resident nodes (N=282).

Modularity of all weekly food webs significantly differed from values expected in random distributions with the same connectance, as 95% confidence intervals excluded the real graph value (Appendix 3). The number of modules detected per web ranged between 1 - 39 (Appendix 4).

Further, all studied species-level graph parameters (node degree and centrality metrics) differed significantly from those of random graphs, as 95% confidence intervals of random networks excluded real network metrics values (Appendix 3).

**Temporal trends in graph metrics**
Temporal distribution of modularity showed a strong nonlinear pattern: the strongest modular networks were observed in January (weeks 1-4), when the presence of migrant taxa is insignificant, whereas trophic networks exhibited only weak modular structure during weeks with migration activity. While winter networks are dominated by trophic interactions established by wintering raptors (especially White-tailed Eagle *Haliaeetus albicilla*, Peregrine Falcon *Falco peregrinus* and Saker Falcons *Falco cherrug*) preying upon wintering waterfowl, passerines and small mammals, trophic networks during the peak migratory periods are enriched by the presence of migrant waterbirds such as herons *Ardeidae*; waders, gulls and marsh terns *Charadriiformes*, dissolving strongly modular structures (Appendix 1). Thus, weak modular structures are observed during February-March and October-November, when waterbird migration is accompanied by eagles and falcons.

Similarly, weekly mean values of all of the studied species-level graph parameters showed highly nonlinear temporal trends: node degree, alpha centrality, betweenness showed high values within the vegetation period and low degrees outside vegetation activity, whereas betweenness and alpha centrality metrics exhibited reverse patterns at within-year scales. (Fig. 2).

*Phylogenetic analyses*

Phylogenetic signal in predator and prey taxonomy was moderate but significant, ranging between 0.0 and 4.425 (mean ± SD = 1.583 ± 0.543) for consumer and between 0.0 and 0.762 (mean ± SD = 0.291 ± 0.253, Fig 3.) for prey taxa, indicating that trophic network structures are conserved along evolutionary lineages (Appendix 5).

*Model selection*

The network properties as a function of migration and phylogeny employing the week-of-year as a fixed factor to control for temporal trends in graph properties, showed the following key relationships. Modularity differed between migrant and resident networks (b = 0.121, p = 0.001): networks including only migratory links were significantly more modular than resident-only networks or pooled datasets during the migratory season ranging between 10-40 week-of-year, suggesting that migrant raptors are more strongly connected to migrant prey items than to resident resources (Fig 3a). Further, modularity was negatively associated with the degree of phylogenetic relatedness of both consumer (b = -0.411, p < 0.0001) and prey (b = -0.165, p = 0.034) (Fig 3b, Table 1), with weak modular structures primarily established by predator-prey interactions of closer related species .

Node degree differed between migration types (b= -9.237, p < 0.0001; Fig 5a) showing larger number of links for migrant species and was positively related to consumer phylogeny
(b=16.768, p < 0.0001), with more related species sharing more links. Alpha centrality differed between migration types (b= -145.462, p = 0.029; Fig 5b): networks including migratory links exhibited larger mean values of alpha centrality than resident-only structures, Further, the degree of alpha centrality was positively associated with both prey (b=389.975, p =0.016) and consumer (b=456.971, p<0.0001) phylogenies, implying that closely related important species establish links to other species that are themselves important. Similarly, mean betweenness was higher for networks including both migratory and resident links than for those separated by migration strategy (b= -8.306, p < 0.0001; Fig 5c) and increased with the degree of consumer phylogeny (b = 16.603, p < 0.0001). Finally, weekly-averaged values of closeness centrality was significantly smaller in networks including migratory links than for resident-only structures (b=0.0001, p=0.001; Fig 5d), and decreased with increasing consumer phylogeny (b=-0.0002, p<0.0001).

Discussion

In the Hortobágy steppe ecosystem we found that: (1) a substantial number of links were established by migrant taxa; (2) the phylogenetic signal in network structure was moderate for both consumer and prey nodes; (3) both consumer and prey phylogenies governed modularity, but this was modulated by migration strategy; and (4) all species-level graph properties significantly differed between networks including and excluding migratory taxa.

Phylogeny

Although we found a modest effect of taxonomic affiliations of both consumer and prey taxa on network structure, the phylogenetic relatedness of consumer species was a key determinant of all network parameters, whereas prey phylogeny was important in determining modularity and alpha centrality. This finding supports the conclusions of previous studies, in which phylogeny has been demonstrated to be the key determinant of food web properties both for the number of resources or predators either shared by any two species or their position in smaller subsets of interacting species within the web (Naisbit et al. 2012; Stouffer et al. 2012, Peralta 2016). Model selection approach showed that consumer phylogeny is a driver of key characteristics of trophic networks in a representative migratory hotspot of a steppe ecosystem. The inclusion of migratory links substantially increased modularity, which implies that closer related migratory consumers more frequently share the same prey items than expected by chance. This pattern has been hypothesised to be the outcome of phylogenetic niche conservatism (Peterson et al. 1999), already demonstrated to exist in network metrics of food webs (Freckleton et al. 2002; Qian & Ricklefs 2004). In contrast,
higher degrees of prey phylogeny was associated only with decreasing levels of modularity and increasing alpha centrality, implying that evolutionary relatedness of prey is less important in governing web structure. This suggests that trophic modules are principally structured by related consumers as well as by preys to a lesser degree, supporting again the existence of processes driven by ecological niche conservatism in food webs (Peterson et al. 1999).

Migration

The fingerprints of migratory movements are inherent in changes in all of our network metrics, strongly nonlinear decreases of which coincide with intense migratory movements of birds and insects. This finding is in line with other studies demonstrating that migratory predator-prey links substantially modulate trophic graph structures, as a result of high levels of synchrony in consumer and prey migration. All studied graph properties significantly differed between networks including and excluding migratory taxa during migration periods. Changes in these network structures over the year suggest that web architecture is influenced by onset and end of vegetation phenology but most importantly, also by migration of insects and birds (Walther et al. 2002): node degree, alpha and betweenness centrality switched from a minimal level in the beginning of the year to a relatively high value between late March and early October. This period embraces the vegetation period and also migratory movements in the region (Ecsedi et al. 2004). This pattern indicates that the sudden nonlinear increase in link numbers, centrality metrics related to the presence of important species as well as modularity is observed not only during spring phenology but also by the less abrupt end of vegetation and migration phenology in autumn (Ecsedi et al 2004). This latter pattern calls for further theoretical studies and the reanalyses of longitudinal observational data in insect and bird phenology, aiming at detecting the realised and predicted effects of current climatic trends on the structure of network architecture.

Networks including migratory species had larger centrality values than those excluding migrants and networks including migratory nodes were also significantly more modular than resident-only networks. This pattern implies that migrant animals move in trophically strongly connected flocks, i.e. migratory consumers/predators follow their migratory prey (Bildstein 2006).

Migratory movements have important consequences for modularity structures. For example, the highest levels of modularity are shown by early spring and late autumn bird migration, involving more than 40 species of waterbirds and passerines as well as their predators. This confirms the importance of migration in governing trophic network systems (Bauer & Hoye 2014).

Interestingly, trophic networks in steppe ecosystems seem to be highly modular outside of the vegetation period and show no clear modular patterns during vegetation activity, which implies that trophically strongly connected species groups exist during continental winters (Chibilyev 2002).
Evidence is mounting that avian raptors synchronize their timing of migration to that of their avian prey, which is especially important in steppe-wetland ecosystems, as the total biomass of migrant avian preys exceeds that of resident birds by a several magnitudes (Alerstam 1993, Elphick 2007, Newton 2010). For example, the breeding of Eleonore’s falcon (*Falco eleonorae*) is highly synchronized with the mass autumn migration of Palearctic birds wintering in Africa (Cramp 1998). Similarly, the Hobby (*Falco subbuteo*) synchronizes its migration to the peak of passerine migratory movements in Eurasia (Leshem & Yom-Tov 1996, Alerstam 2011).

We believe that our results are of relevance for other trophic networks in migratory hotspots, with a special respect to coastal and steppe ecosystems, harbouring a number of threatened migratory species (Bauer & Hoye 2014). This calls for further investigations on the applicability of food webs in management of migratory hotspots. In sum, we have demonstrated that the structure of steppe trophic networks is primarily governed by migration strategies and to a lesser extent by phylogenetic relatedness, using the largest available food web representative for steppe ecology and migration biology.

**Declarations**

The first and second author contributed equally to this paper.
References


**Tables.**

**Table 1.** Results of model selection of GLM-s fitted on network parameters as a function of week, migration strategy as well as consumer and prey phylogeny of Hortobágy steppe network, calculated across models of substantial support (ΔAICc < 2.0). Significant relationships are indicated in bold, as provided by z-statistic of predictor importance.

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<td>3.50863</td>
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<td>2.24524</td>
<td>4.11409</td>
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</table>

**Centrality metrics**

|                   | Intercept                  | -171.78266 | 146.03890 | 146.61533 | 1.17166 | 0.24134 |
|                   | Migration (migrant)       | -145.46179 | 66.12570  | 66.65994  | 2.18215 | 0.02910 |
|                   | Migration (non-migrant)   | -134.75422 | 64.85308  | 65.37704  | 2.06119 | 0.03929 |
|                   | Consumer phylogeny        | 456.97128  | 64.55973  | 64.99598  | 7.03076 | <0.0001 |
|                   | Prey phylogeny            | 389.97484  | 161.01481 | 161.79579 | 2.41029 | 0.01594 |

|                   | Intercept                  | 6.08823   | 3.88291  | 3.90034     | 1.56095 | 0.11854 |
|                   | Migration (migrant)       | -8.86320  | 2.25238  | 2.26675     | 3.91008 | 0.00009 |
|                   | Migration (non-migrant)   | -8.25189  | 2.20928  | 2.22362     | 3.71101 | 0.00021 |
|                   | Consumer phylogeny        | 16.60300  | 2.06914  | 2.08310     | 7.97033 | <0.0001 |
|                   | Prey phylogeny            | 6.81602   | 4.66966  | 4.70738     | 1.44794 | 0.14763 |
|                   | Week                      | 0.02208   | 0.04851  | 0.04891     | 0.45146 | 0.65166 |

<p>|                   | Intercept                  | 0.00002   | 0.00000  | 0.00000     | 7.44238 | &lt;0.0001 |
|                   | Migration (migrant)       | 0.00001   | 0.00000  | 0.00000     | 3.18545 | 0.00145 |
|                   | Migration (non-migrant)   | 0.00001   | 0.00000  | 0.00000     | 2.90893 | 0.00363 |
|                   | Consumer phylogeny        | -0.00002  | 0.00000  | 0.00000     | 6.21924 | &lt;0.0001 |</p>
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**Figure legends.**

**Fig 1.** Time-aggregated structure of the Hortobágy trophic network, indicating the dominance of migratory links between orders. Black nodes indicate links with more migratory links than resident connections, whereas grey nodes represent links dominated by resident associations. Order names are abbreviated to the first three characters.

**Fig 2.** Within-year temporal change of graph parameters derived from trophic networks in Hortobágy steppe ecosystem.

**Fig 3.** The strength of phylogenetic signal for consumers and preys.

**Fig 4.** Modularity of Hortobágy trophic networks over time as a function of (a) migration type and (b) as dependent on consumer and prey phylogeny.

**Fig 5.** Significant relationships between a) mean node degree; b) mean alpha centrality; c) mean betweenness; and d) mean closeness centrality, as well as migration type for the Hortobágy trophic network.
Fig 1.
Fig 2.

![Graphs showing the changes in degree, alpha centrality, betweenness centrality, and modularity over the weeks.](image-url)
Fig. 3.
Fig 4.

(a)

(b)
Fig 5.