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

2

3 **Abstract**

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5   Evidence is mounting that the structures of trophic networks are governed by migratory

6 movements of interacting species and also by their phylogenetic relationships. Using the largest

7 available trophic network of a large steppe ecosystem, we tested that steppe trophic networks

8 including migratory species are associated with (i) migratory strategy and (ii) phylogenetic

9 relatedness of interacting species: (1) whole graph-level metrics, estimated as modularity, and (2)

10 species-level network metrics, measured as node degree (number of interacting partners), and

11 centrality metrics. We found that (1) a substantial number of links were established by migrant taxa;

12 (2) the phylogenetic signal in network structure was moderate for both consumer and prey nodes;

13 (3) both consumer and prex phylogenies affected modularity, which was modulated by migration

14 strategy; and (4) all species-level graph properties significantly differed between networks

15 including and excluding migratory taxa. In sum, here we show that the structure of steppe trophic

16 networks is primarily governed by migratory strategies and to a lesser extent, by phylogenetic

17 relatedness, using the largest available food web representative for steppe ecology and migration

18 biology.

19

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

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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 westernmost 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 westernmost 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.

90   Furthermore, the region is acknowledged as the most important stopover site and wintering area

91   along the Baltic-Hungarian Flyway harbouring significant populations of European waterbirds,

92   waders, raptors and passerines (Ecsedi et al 2004, Végvári et al. 2010, Mingozzi et al. 2013). Our

93   dataset contains information on 53 bird species, which occur only as migrant in the study area.

94   To assemble the trophic web, we used all known direct trophic interactions, i.e. consumer-

95   prey relatedness among co-occuring species based on expert knowledge derived from literature data

96   and our own observations in the Hortobágy steppe region (Mahunka 1981, Szujkó-Lacza 1981,

97   Ecsedi et al 2004). These works cover four decades and provide replicated estimates on presence-

98   absence data with representative spatial coverage of the Hortobágy steppe. Thus, our network

99   included all species which co-occur during reproduction, migration or wintering in the Hortobágy

100   steppe (see Ecsedi et al. 2004 and Végvári et al. 2010 for sampling methodology and taxon list, see

101   Appendix 1 for species list and migration types (migratory or resident). Due to limited information,

102   our dataset excludes parasites, amphipods and isopods.The trophic network is time-integrated on a

103   weekly time-scale, thus providing 52 networks representing all weeks of the year (Kéfi et al. 2015).

104   We constructed species-by-species matrices for trophic interactions for each week of the

105   year, coded as 0 or 1 (species i feeds on species j or not, which are evidently unidirectional effects

106   of species i on species j (Appendix 1). The final matrix of these interactions yields the most

107   comprehensive description of trophic interactions among all 535 species of the Eurasian steppe

108   ecosystem. The dataset is available in an editable, annotatable, and shareable cloud-based network

109   visualization software (available online at the Dryad Data Repository - .https://datadryad.org/)

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114   *Network parameters*

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116   For each weekly aggregated network, we calculated several network characteristics,

117   capturing different aspects of the biological significance of each species to the food web (González

118   et al 2010, Kéfi et al. 2015).

119   (1) We quantified network structure by identifying modules, defined as strongly

120   interconnected groups of nodes which are only weakly linked to other highly connected groups

121   (Guimera & Amaral 2005). Modularity is a metric of the proportion of edges located within

122   modules minus the the expected value in a similarly structured random network with random links,

123   ranging between 0.0 and 1.0, where 1.0 is assigned to a perfectly modular network, i.e. zero stands

124   for no subgroups, whereas 1 indicates totally separated subgroups.

125   (2) We further calculated weekly-averaged mean values of species-level network metrics,

126 representatively describing food webs:

127   (a) node degree , calculated as the sum of incoming and outgoing links, including all preys

128 and predators of a given taxon.

129   (b) Centrality indices, that characterize the importance of single nodes or links in the

130 network (Paulau et al 2015): (i) closeness centrality, defined as the inverse of the mean shortest path

131 length from a species to all the other species in the network, which indicates important nodes that

132 can communicate quickly with other nodes of the network (Pavlopoulos et al. 2011); (ii)

133 betweenness centrality, calculated as the extent to which a focal species lies on the shortest paths

134 between two other species, which shows that nodes which are intermediate between neighbors rank

135 higher. Without these nodes, two neighbors would not be able to be connected to each other

136 (Pavlopoulos et al. 2011). Thus, betweenness centrality shows important nodes that lie on a high

137 proportion of paths between other nodes in the network (Freeman 1979); finally, (iii) alpha

138 centrality, which is an adaptation of eigenvector centrality measuring the species' importance based

139 on whether it has connections to other species that are themselves important; alpha centrality

140 enhances this process by allowing nodes to have external sources of influence.

141

142 *Statistical analyses*

143

144 <u>Non-randomness</u>

145   The above graph metrics were also calculated for 10000 random networks with the same

146 overall connectivity as the empirical network to assess whether the empirical food web statistically

147 differed from random networks (Guimerà et al. 2004, Kéfi et al. 2015). If a specific measure from

148 the empirical network lay outside mean $\pm$ SD of that measure in the random network, we assumed it

149 statistically differed (Bornatowski et al. 2017).

150

151 <u>Phylogeny</u>

152 In the absence of a complete molecular phylogeny for all species included within our trophic

153 network, each species was classified into a nested taxonomic hierarchy including family, order,

154 class and phylum, based on the comprehensive systematic classification from the Tree of Life

155 (Letunic & Bork 2006).   To quantify the phylogenetic signal of networks, we fitted a generalized

156 linear mixed model (Peralta 2016), using connection type (connected or unconnected links defined

157 on the complete set of studied species) as binary response, and the taxonomic class of consumer

158 (belonging to N = 115 families) and prey species (classified into N = 142 families), both employed

159 as a hierarchically nested random factor, defined as kingdom/phylum/class/order/family, applying

160 binomial logit link. In the next step, the degree of phylogenetic dependence was measured as the

161 variance explained by the nested random terms. This metric of taxonomic heritability is considered

162 as an estimate of the phylogenetic signal in the data. (Nakagawa & Schielzeth 2013; Kéfi et al.

163 2015).

164

165 <u>Effects of migration and phylogeny network topology</u>

166 To estimate the effects of migratory strategy and phylogenetic relatedness on present

167 network topology, we formulated linear models for each graph metric using the degree of

168 phylogenetic relatedness among consumer and prey species (calculated as the variance of the nested

169 random term defined in Phylogeny subsection), week and migration strategy (separated for

170 strategies and pooled) as fixed predictors. The importance of these predictors was evaluated

171 applying AIC-based model selection within the information-theoretic framework (Kenneth et al.

172 2002).

173 All analyses were run with R 3.1.0, including the "igraph" package for calculating network

174 properties (Csárdi & Nepusz 2006)

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176

177 **Results**

178

179 *Distribution and non-randomness of network properties*

180

181 Out of the 289962 edges of the trophic network of Hortobágy steppe ecosystem, 23867 (8.2%)

182 included at least one node represented by a migrant species. While migrant nodes were constituted

183 by 247 genera, resident links were generated by 467 genera (Appendix 1-2, Fig 1). Consumer

184 species of migrant nodes included 34 genera (all birds), which amounted to 12.1% that of resident

185 nodes (N=282).

186 Modularity of all weekly food webs significantly differed from values expected in random

187 distributions with the same connectance, as 95 % confidence intervals excluded the real graph value

188 (Appendix 3). The number of modules detected per web ranged between 1 - 39 (Appendix 4).

189 Further, all studied species-level graph parameters (node degree and centrality metrics)

190 differed significantly from those of random graphs, as 95% confidence intervals of random

191 networks excluded real network metrics values (Appendix 3).

192

193 *Temporal trends in graph metrics*

194

195   Temporal distribution of modularity showed a strong nonlinear pattern: the strongest

196   modular networks were observed in January (weeks 1-4), when the presence of migrant taxa is

197   insignificant, whereas trophic networks exhibited only weak modular structure during weeks with

198   migration activity.   While winter networks are dominated by trophic interactions established by

199   wintering raptors (especially White-tailed Eagle *Haliaaetus albicilla,* Peregrine *Falco peregrinus*

200   and Saker Falcons *Falco cherrug*) preying upon wintering waterfowl, passerines and small

201   mammals, trophic networks during the peak migratory periods are enriched by the presence of

202   migrant waterbirds such as herons *Ardeidae;* waders, gulls and marsh terns *Charadriiformes,*

203   dissolving strongly modular structures (Appendix 1). Thus, weak modular structures are observed

204   during February-March and October-November, when waterbird migration is accompanied by

205   eagles and falcons.

206   Similarly, weekly mean values of all of the studied species-level graph parameters showed

207   highly nonlinear temporal trends: node degree, alpha centrality, betweenness showed high values

208   within the vegetation period and low degrees outside vegetation activity, whereas betweenness and

209   alpha centrality metrics exhibited reverse patterns at within-year scales. (Fig. 2).

210

211   *Phylogenetic analyses*

212   Phylogenetic signal in predator and prey taxonomy was moderate but significant, ranging

213   between 0.0 and 4.425 (mean ± SD = 1.583 ± 0.543) for consumer and between 0.0 and 0.762

214   (mean ± SD = 0.291 ± 0.253, Fig 3.) for prey taxa, indicating that trophic network structures are

215   conserved along evolutionary lineages (Appendix 5).

216

217   *Model selection*

218   The network properties as a function of migration and phylogeny employing the week-of-

219   year as a fixed factor to control for temporal trends in graph properties, showed the following key

220   relationships. Modularity differed between migrant and resident networks (b = 0.121, p = 0.001):

221   networks including only migratory links were significantly more modular than resident-only

222   networks or pooled datasets during the migratory season ranging between 10-40 week-of-year ,

223   suggesting that migrant raptors are more strongly connected to migrant prey items than to resident

224   resources (Fig 3a). Further, modularity was negatively associated with the degree of phylogenetic

225   relatedness of both consumer (b = -0.411, p < 0.0001) and prey (b = -0.165, p = 0.034) (Fig 3b,

226   Table 1), with weak modular structures primarily established by predator-prey interactions of closer

227   related species .

228   Node degree differed between migration types (b= -9.237, p < 0.0001; Fig 5a) showing

229   larger number of links for migrant species and was positively related to consumer phylogeny

230 (b=16.768, p < 0.0001), with more related species sharing more links . Alpha centrality differed

231 between migration types (b= -145.462, p = 0.029; Fig 5b): networks including migratory links

232 exhibited larger mean values of alpha centrality than resident-only structures, Further, the degree of

233 alpha centrality was positively associated with both prey   (b=389.975, p =0.016) and consumer

234 (b=456.971, p<0.0001)   phylogenies, implying that closely related important species establish

235 links to other species that are themselves important. Similarly, mean betweenness was higher for

236 networks including both migratory and resident links than for those separated by migration strategy

237 (b=-8.306, p < 0.0001; Fig 5c) and increased with the degree of consumer phylogeny (b = 16.603, p

238 < 0.0001). Finally, weekly-averaged values of closeness centrality was significantly smaller in

239 networks including migratory links than for resident-only structures (b=0.0001, p=0.001; Fig 5d),

240 and decreased with increasing consumer phylogeny (b=-0.0002, p<0.0001).

241

242

243 **Discussion**

244

245   In the Hortobágy steppe ecosystem we found that: (1) a substantial number of links were

246 established by migrant taxa; (2) the phylogenetic signal in network structure was moderate for both

247 consumer and prey nodes;   (3) both consumer and prey phylogenies governed modularity, but this

248 was modulated by migration strategy; and (4) all species-level graph properties significantly

249 differed between networks including and excluding migratory taxa.

250

251 *Phylogeny*

252   Although we found a modest effect of taxonomic affiliations of both consumer and prey taxa

253 on network structure, the phylogenetic relatedness of consumer species was a key determinant of all

254 network parameters, whereas prey phylogeny was important in determining modularity and alpha

255 centrality. This finding supports the conclusions of previous studies, in which phylogeny has been

256 demonstrated to be the key determinant of food web properties both for the number of resources or

257 predators either shared by any two species or their position in smaller subsets of interacting species

258 within the web (Naisbit et al. 2012; Stouffer et al. 2012, Peralta 2016). Model selection approach

259 showed that consumer phylogeny is a driver of key characteristics of trophic networks in a

260 representative migratory hotspot of a steppe ecosystem. The inclusion of migratory links

261 substantially increased modularity, which implies that closer related migratory consumers more

262 frequently share the same prey items than expected by chance. This pattern has been hypothesised

263 to be the outcome of phylogenetic niche conservatism (Peterson et al. 1999), already demonstrated

264 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 trophicly 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*) synchronises 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.

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Tables.

457 **Table 1.** Results of model selection of GLM-s fitted on network parameters as a function of week,

458 migration strategy as well as consumer and prey phylogeny of Hortobágy steppe network,

459 calculated across models of substantial support (ΔAICc < 2.0). Significant relationships are

460 indicated in bold, as provided by z-statistic of predictor importance.

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Network parameter	Predictor	Estimate	SE	Adjusted SE	Z-score	p
Node degree	Intercept	12.67539	3.59377	3.61263	3.50863	**0.00045**
	Migration (migrant)	-9.23709	2.22971	2.24524	4.11409	**0.00004**
	Migration (non-migrant)	-8.77446	2.19560	2.21105	3.96846	**0.00007**
	Consumer phylogeny	16.76817	2.07130	2.08627	8.03739	**< 0.00001**
	Prey phylogeny	5.50304	4.87565	4.91504	1.11963	0.26287
Centrality metrics						
Alpha centrality	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	**<0.00001**
	Prey phylogeny	389.97484	161.01481	161.79579	2.41029	**0.01594**
Betweenness centrality	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	**< 0.00001**
	Prey phylogeny	6.81602	4.66966	4.70738	1.44794	0.14763
	Week	0.02208	0.04851	0.04891	0.45146	0.65166
Closeness centrality	Intercept	0.00002	0.00000	0.00000	7.44238	**< 0.00001**
	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	**< 0.00001**

	Week	0.00000	0.00000	0.00000	0.95815	0.33799
Modularity	Intercept	0.73825	0.06574	0.06627	11.13970	**< 0.00001**
	Migration (migrant)	0.12147	0.03727	0.03757	3.23302	**0.00122**
	Migration (non-migrant)	-0.04407	0.03647	0.03677	1.19856	0.23070
	Consumer phylogeny	-0.41052	0.03417	0.03444	11.91901	**< 0.00001**
	Prey phylogeny	-0.16463	0.07703	0.07765	2.12006	**0.03400**
	Week	-0.00093	0.00080	0.00080	1.16201	0.24523

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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.
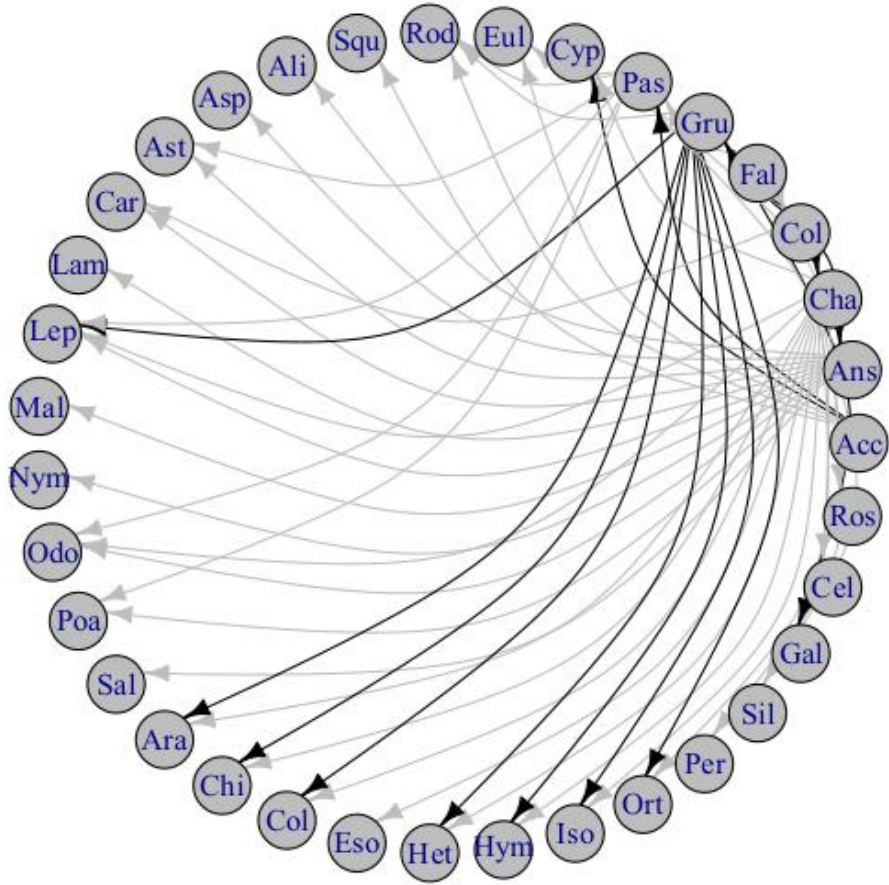
488   **Fig 2.**

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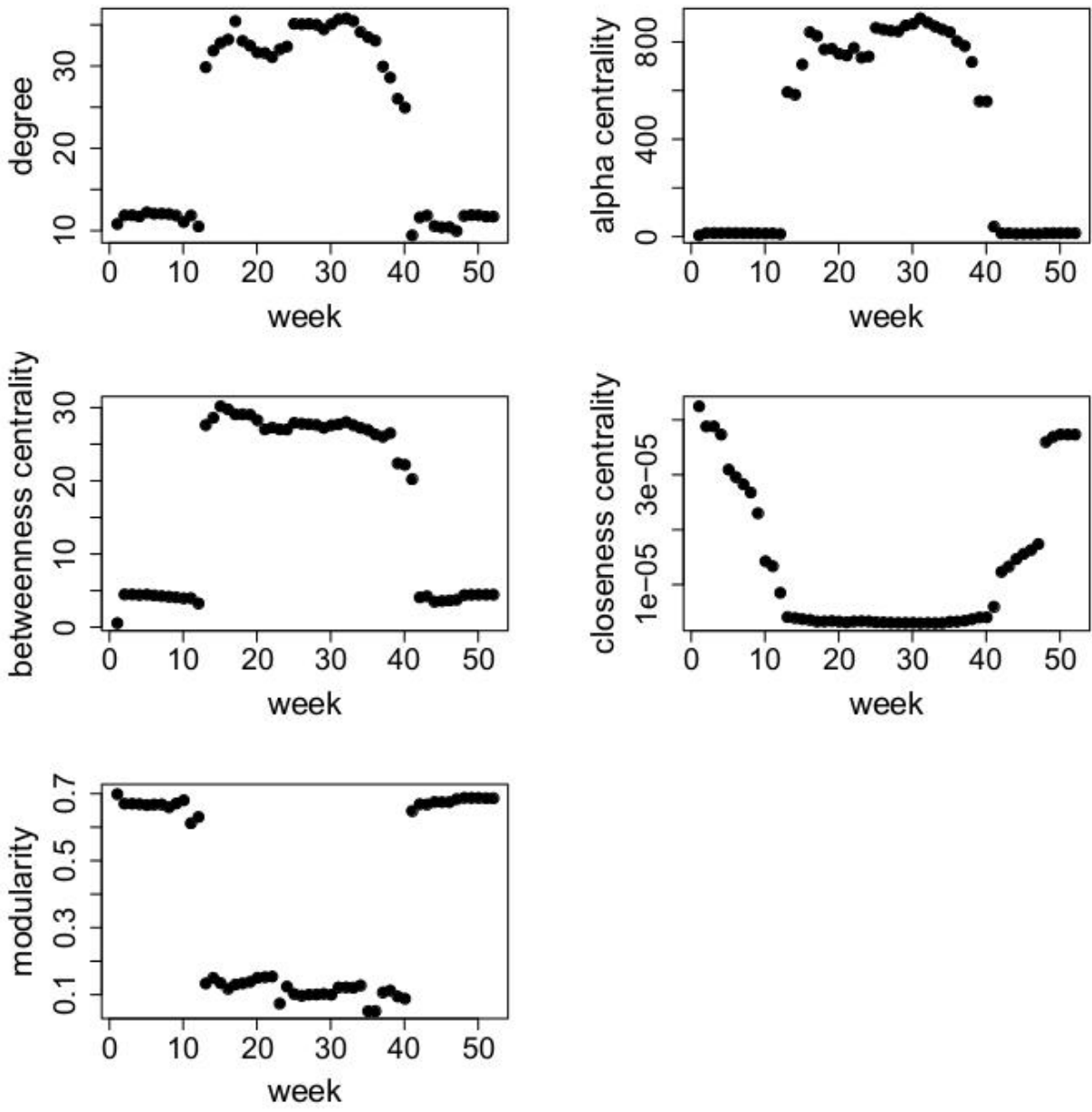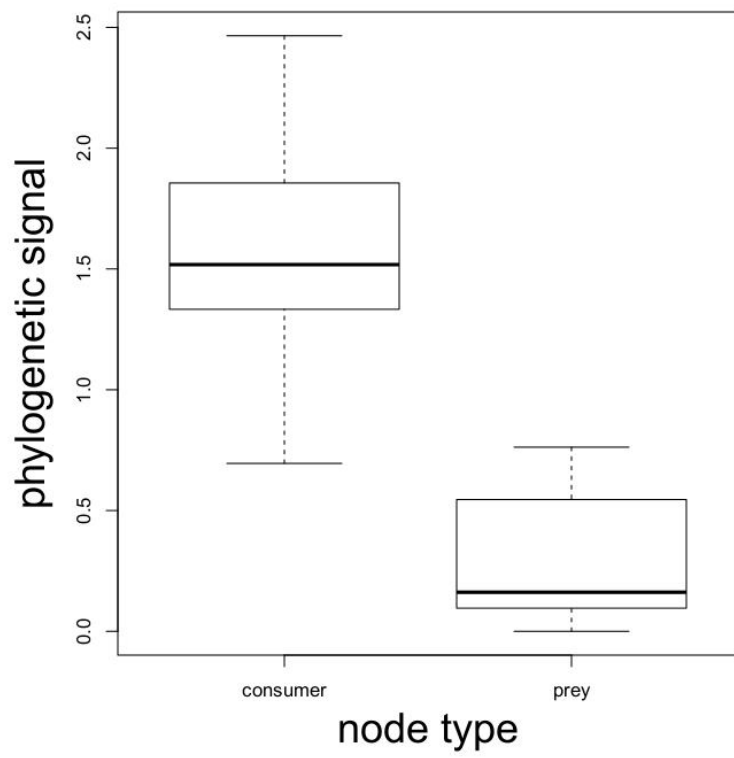

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492 **Fig.3.**

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494 **Fig 4.**

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496   (a)   (b)
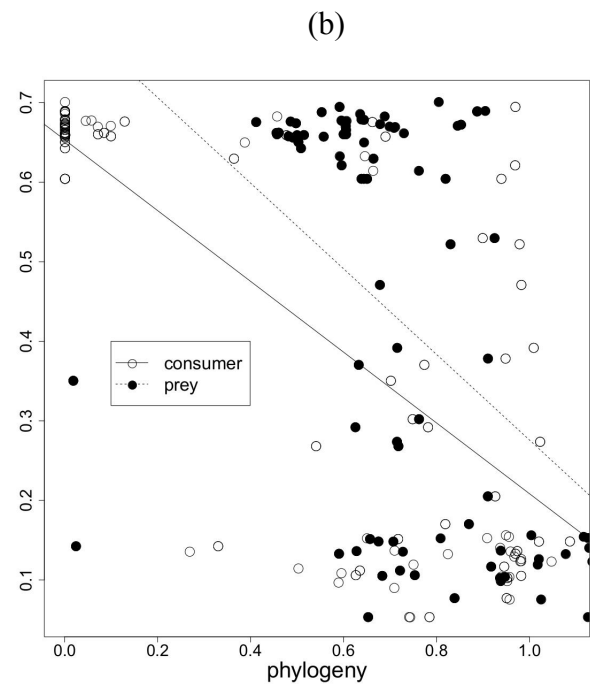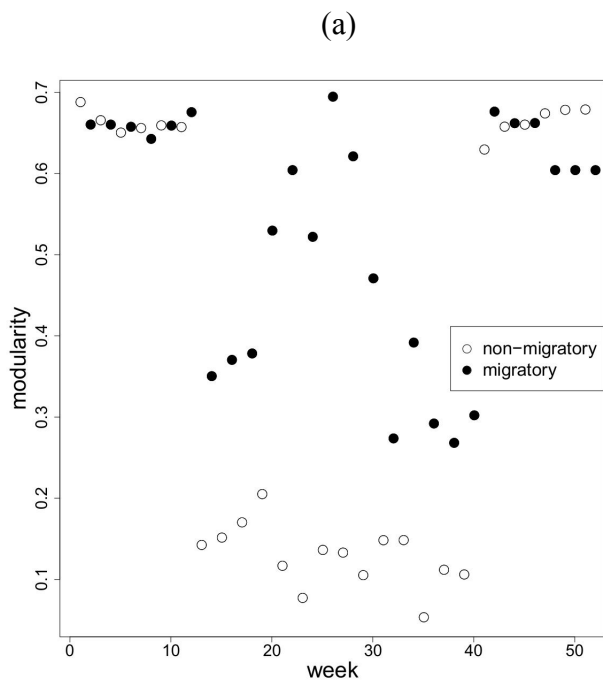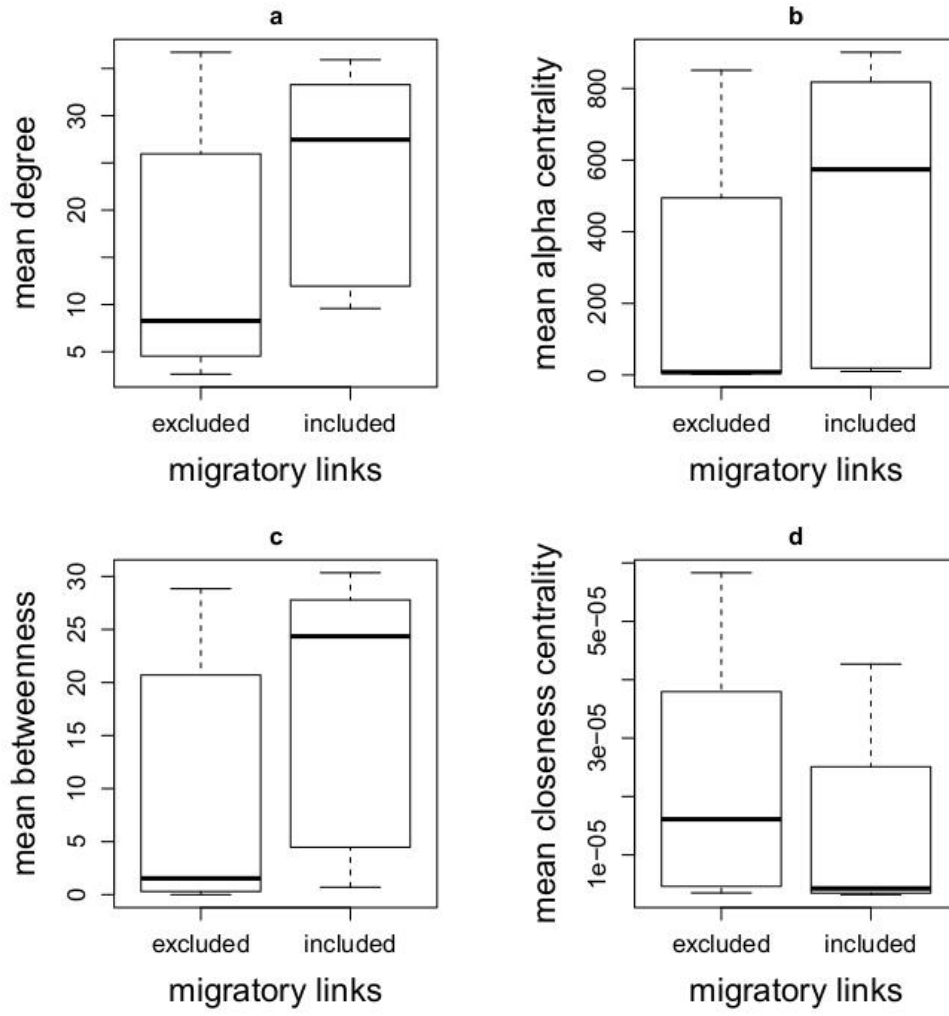

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Fig 5.

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