

Article (refereed) - postprint

Hui, Cang; Richardson, David M.; Landi, Pietro; Minoarivelo, Henintsoa O.; Garnas, Jeff; Roy, Helen E. 2016. **Defining invasiveness and invisibility in ecological networks.** *Biological Invasions*, 18 (4). 971-983. [10.1007/s10530-016-1076-7](https://doi.org/10.1007/s10530-016-1076-7)

© Springer International Publishing Switzerland 2016

This version available <http://nora.nerc.ac.uk/513373/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. There may be differences between this and the publisher's version. You are advised to consult the publisher's version if you wish to cite from this article.

The final publication is available at Springer via
<http://dx.doi.org/10.1007/s10530-016-1076-7>

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 Defining invasiveness and invasibility in ecological networks

2

3 Cang Hui^{1,2,*},

4 David M. Richardson³,

5 Pietro Landi^{1,4},

6 Henintsoa O. Minoarivelo¹,

7 Jeff Garnas⁵,

8 Helen E. Roy⁶

9

10

11 ¹ Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University,
12 Matieland 7602, South Africa;

13 ² BioMath Group, African Institute for Mathematical Sciences, Cape Town 7652, South
14 Africa;

15 ³ Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University,
16 Matieland 7602, South Africa;

17 ⁴ Evolution and Ecology Program, International Institute for Applied Systems Analysis,
18 Schloßplatz 1, 2361 Laxenburg, Austria;

19 ⁵ Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute,
20 University of Pretoria, Pretoria 0002, South Africa;

21 ⁶ Centre for Ecology & Hydrology, Wallingford, Oxfordshire, OX10 8BB, UK

22

23 * Correspondence: E-mail: chui@sun.ac.za

24

25 **Abstract**

26 The success and failure of a biological invasion is context based, and yet two key concepts –
27 the invasiveness of species and the invasibility of recipient ecosystems - are often defined and
28 considered separately. We propose a framework that can elucidate the complex relationship
29 between invasibility and invasiveness. It is based on trait-mediated interactions between
30 species and depicts the response of an ecological network to the intrusion of an alien species
31 drawing on the concept of community saturation. Here, invasiveness of an introduced species
32 with a particular trait is measured by its per capita population growth rate when the initial
33 propagule size of the introduced species is very small. The invasibility of the recipient habitat
34 or ecosystem is dependent on the structure of resident ecological network and is defined as
35 the total width of opportunity niche in the trait space susceptible to invasion. Invasibility is
36 thus a measure of network instability. We also correlate invasibility with the asymptotic
37 instability of resident ecological network, measured by the leading eigenvalue of the
38 interaction matrix that depicts trait-based interaction intensity multiplied by encounter rate (a
39 pairwise product of propagule sizes of all members in a community). We further examine the
40 relationship between invasibility and network architecture, including network connectance,
41 nestedness and modularity. We exemplify this framework with a trait-based assembly model
42 under perturbations in ways to emulate fluctuating resources and random trait composition in
43 ecological networks. The maximum invasiveness of a potential invader was found to be
44 positively correlated with invasibility of the recipient ecological network. Additionally,
45 ecosystems with high network modularity and high ecological stability tend to exhibit high
46 invasibility. Where quantitative data are lacking we propose using a qualitative interaction
47 matrix of the ecological network perceived by a potential invader so that the structural
48 network stability and invasibility can be estimated from literature or from expert opinion. This
49 approach links network structure, invasiveness and invasibility in the context of trait-mediated
50 interactions, such as the invasion of insects into mutualistic and antagonistic networks.

51

52 **Keywords:** biological invasions, fluctuating resource hypothesis, invasiveness, invasibility,
53 ecological networks, interaction matrix, network stability, interaction strength

55 **1. Introduction**

56 The search for generality in invasion ecology has progressed largely through quantifying the
57 drivers behind two concepts separately and in concert: the invasiveness of alien species and
58 the invasibility of recipient ecosystems (Richardson and Pyšek 2006). The concept of
59 invasiveness follows a species-centric view of the introduction-naturalisation-invasion
60 continuum (Blackburn et al. 2011). Much of the study of invasiveness has involved the
61 identification and exploration of traits, barriers and drivers that determine location on this
62 continuum for a given taxon (Richardson and Pyšek 2012). Invasiveness, or the propensity of
63 invasive alien species (hereafter IAS) to invade, can be identified from comparative metrics
64 between invasive and non-invasive alien species, such as those related to translocation bias,
65 propagule pressure, and foraging/reproduction/dispersal traits (Pyšek and Richardson 2007).
66 Invasiveness is further related to the potential impacts of IAS on the function and service of
67 recipient ecosystems and thus dictates the prioritisation, prevention and control strategies in
68 response to biological invasions (Blackburn et al. 2014). Of particular importance are the
69 suite of traits of IAS that differ from those of native species and non-invasive alien species. A
70 trait-based priority list of potentially highly invasive species can then be developed (Peacock
71 and Worner 2008; Moravcová et al. 2015).

72 The second concept – invasibility – is a property of recipient ecosystems and involves
73 the elucidation of features that determine its vulnerability to invasion such a community
74 diversity, composition and assembly (Lonsdale 1999). Community assembly rules outline
75 how species are “packed” in a community and how community composition is related to the
76 occupied and available niche space in a given community. Early niche theories gave special
77 attention to the role of biotic interactions in structuring communities (Tilman 2004). More
78 recently, recognition that species assemblages in unsaturated local communities are at least in
79 part driven by neutral forcing via the continuous influx of regional and alien species (Hubbell
80 2001; Stohlgren et al. 2003). Despite contrasting opinions on the applicability of neutral
81 theory to real world communities (Chase 2005; Clark 2012; Rosindell et al. 2012), it is now
82 widely accepted that both deterministic and stochastic processes interact to structure species
83 assemblages (Bar-Massada et al. 2014; Nuwagaba et al. 2015).

84 To further elucidate the concept of invasibility, it is essential to first determine how an
85 ecosystem responds to perturbations such as biological invasions, an issue that has been
86 debated at least since May’s (1974) proposition that complexity begets instability (McCann
87 2000; Fridley 2011, Allesina and Tang 2012). As the recipient ecosystem often comprises

88 many interacting species, an ecological network provides an effective model for exploring the
89 inherent complexity. A key aspect of this debate thus relates to connecting the different
90 perspectives of network architecture to the stability of ecological networks. The architecture
91 of an ecological network can be measured as particular features of the interaction matrix,
92 depicting whether and how strongly two nodes interact. Typical features include connectance
93 (the proportion of realized interactions among all possible ones; Olesen and Jordano 2002),
94 nestedness (specialists only interacting with a subset of species with which generalists interact;
95 Bascompte et al. 2003) and compartmentalization (a network can be grouped into delimited
96 modules, measured by the level of modularity, where species are strongly interacting with
97 species within the same module but not those from other modules; Newman 2006). Network
98 complexity normally refers to a combined factor of network size (the number of nodes) and
99 connectance (May 1974; Allesina and Tang 2012). Although consensus on the structure of
100 mutualistic networks has been reached (e.g. Bascompte et al. 2003; Olesen et al. 2007;
101 Guimarães et al. 2007; Thébault and Fontaine 2010; Mello et al. 2011), there is still
102 considerable debate with respect to antagonistic networks (e.g., on whether antagonistic
103 networks are more compartmentalised than random expectation; e.g. Poisot 2013).

104 Network stability, in contrast to network architecture, concerns how networks respond
105 to perturbations (Yodzis 1981) and can be measured using different approaches (i.e.,
106 Lyapunov asymptotic stability, resilience, persistence and robustness, among others; May
107 1974; Pimm and Lawton 1978; Dunne et al. 2002; Donohue et al. 2013). The analysis of
108 Lyapunov stability is a long established mathematical tool in dynamical systems for depicting
109 whether a complex system will return to its local equilibrium after weak perturbations; this is
110 typically assessed as the leading eigenvalue of the interaction matrix (May 1974; Allesina and
111 Tang 2012). Such perturbations in an ecological network are often manifested as changes in
112 population sizes caused by stochasticity or changing resources (Davis et al. 2000). Recent
113 progress in resolving the complexity-stability debate has involved exploring the causal
114 relationship between the architecture and stability of many mutualistic (e.g., plant-frugivore
115 and plant-pollinator), trophic (food web) and antagonistic (predator-prey and host-
116 parasite/pathogen) networks (e.g. Memmott et al. 2004; Eklof and Ebenman 2006; Bascompte
117 et al. 2006; Burgos et al. 2007; Estrada 2007; Bastola et al. 2009; Kiers et al. 2010; Thébault
118 and Fontaine 2010; Brose 2011; de Visser et al. 2011; Stouffer and Bascompte 2011; James et
119 al. 2012), and explaining emergent network structures using dynamic network models with
120 adaptive and random species rewiring (van Baalen et al. 2001; Kondoh 2003; Rezende et al.
121 2007; Vacher et al. 2008; Valdovinos et al. 2010; Zhang et al. 2011; Suweis et al. 2013;
122 Minoarivelo et al. 2014; Nuwagaba et al. 2015).

123 Here, we introduce *invasibility* as a new aspect of network instability. Full
124 comprehension of the proposed framework of invasiveness and invasibility in ecological
125 networks requires us first to establish the concept of *community saturation* in a network. This
126 concept was initially developed from the theory on competition and limiting similarity
127 (MacArthur 1972; Abrams 1983) where strong interspecific interactions preclude the
128 establishment of IAS. A saturated ecological network can be defined as a particular
129 community assemblage (a suite of species with their particular traits and population sizes) that
130 cannot be invaded by an alien species given low propagule number, irrespective of that
131 species' life history or relevant traits. Certainly, when the propagule size is too large, system
132 behaviour will be overridden by the influx of propagules, making the concept of invasibility
133 irrelevant. Very few, if any, ecological networks are truly saturated, as local communities can
134 be strongly affected by regional species dynamics and stochasticity (Abrams 1998; Loreau
135 2000); rather the concept of community saturation serves as a theoretical benchmark by which
136 invasibility can be measured. Specifically, the deviation from a saturated community can be
137 measured by the cumulative niche space that permits invasion for a given recipient ecosystem.

138 Invasibility and invasiveness are not isolated concepts but are strongly interwoven. As
139 an example, as Darwin (1859) first posited in what has become known as his “naturalization
140 hypothesis”, introduced species should be more successful (i.e., more invasive) when the
141 recipient community lacks congeneric or ecologically similar species (Duncan and Williams
142 2002). The underlying logic of this statement relies on the assumption that closely related
143 species show greater life history, trait and therefore niche overlap such that an intact
144 community would be minimally invadable to congeners relative to more distantly related
145 species. A counter-argument which has received some empirical support is that trait similarity
146 among related species might predict habitat suitability and result in higher invasibility when
147 congeners are considered (Duncan and Williams 2002). Either way, it is clear that the two
148 core concepts – invasibility and invasiveness – are context dependent and closely related.
149 Moreover, introduced species can often only invade certain native ecosystems following some
150 form of perturbation (Davis et al. 2000; Shea and Chesson 2002). Here, we attempt to
151 explicitly bridge these two concepts through trait-mediated interactions in ecological
152 networks by visualising both in a single invasion fitness diagram. Since this is a new aspect of
153 network instability, we also examine how invasibility is related to other network stability
154 measures (specifically asymptotic stability), and how it is related to typical network structure.
155 We exemplify this framework using a trait-mediated assembly-level model and discuss how
156 invasibility can be practically assessed with poor data quality by using qualitative interaction
157 matrix, in cases for selected invasive alien insects in a variety of ecosystems.

159 **2. Invasion fitness**

160 Assembly-level models have a long history in community ecology (e.g. Drake 1990; Morton
161 and Law 1997) and they normally assume infrequent colonization of new species from a pre-
162 determined regional species pool. Some recent assembly-level models further allow limited
163 evolutionary processes (e.g. Drossel et al. 2001; McKane 2004) and adaptive response to
164 disturbance (Kondoh 2003; Zhang et al. 2011; Suweis et al. 2013; Nuwagaba et al. 2015;
165 Minoarivelo and Hui 2015; Hui et al. 2015). In particular, the model proposed by Loeuille and
166 Loreau (2005) can depict the emergence of complex food webs through ecological and
167 evolutionary processes involving trait-mediated interactions. Here, we use a food-web model
168 with trait-mediated interactions to demonstrate the framework of invasiveness and invasibility.
169 Specifically, we consider a generalised version of the Loeuille and Loreau (2005) model
170 developed by Brännström et al. (2011) which depicts the per capita population change rate as
171 a function of population growth derived from prey consumption minus mortality from
172 senescence, predation and interference competition (Appendix A). This model is applied
173 because assembly-level data on functional traits, population sizes and interaction strengths are
174 often lacking, which precludes the study of a full network. Simply, targeting functional traits
175 that appear especially important to the population demography of focal species (i.e., that
176 affect the strength of density dependence or influence biotic interactions) makes model
177 parameterization more tractable. Certainly, the absence of such data hampers the clarity when
178 introducing the framework of network invasibility. For this reason, in what follows we will
179 not discuss details of the model itself. Rather, we focus on introducing the framework with
180 this model only serving as a tool for generating required data. In the absence of
181 comprehensive knowledge of communities and community interactions, all is not lost – we
182 discuss the protocol for cases with insufficient data later. As we shall see, even only
183 characterizing the directionality of interactions among species without estimates of interaction
184 strength can be effective in quantifying invasiveness and invasibility (Rossberg et al. 2010).

185 Generating a resident network of multiple heterotrophic species as depicted in the
186 model (Appendix A) can be accomplished in two ways. First, many studies have followed a
187 simple procedure of randomly assigning trait values and parameters for all initial species,
188 running the model until equilibrium is reached, and then removing those species with
189 population sizes below a certain threshold (Holland and DeAngelis 2010). At this stage the
190 network is considered to be at its equilibrium. Once the recipient community has reached its
191 equilibrium, we could consider the invasiveness of a potential introduced species as its

192 *invasion fitness*, defined as its per-capita population growth rate when propagule size is trivial
193 (close to zero) and the community is at equilibrium (Fig.1a). Invasion fitness is a good proxy
194 of invasiveness for an introduced species – if the trait of an introduced species lies within the
195 green intervals along the zero invasion fitness line (Fig.1a), the introduced species will
196 experience positive invasion fitness and thus be able to establish and invade the resident
197 community. If trait values land within the yellow intervals, the species will experience
198 negative invasion fitness and thus be repelled by the resident community (Fig.1a). Clearly, not
199 all species can invade the resident network (Fig.1a).

200 For a given introduced species with a particular trait, if there is a native resident
201 species having an identical/similar trait (i.e. the trait of introduced species is close to any one
202 red dot [traits of resident species] in Fig.1a), the invasion fitness will then become close to
203 zero. Because of the zero population growth, such species are less likely to establish simply
204 due to demographic stochasticity (the case of neutral coexistence). Even if these species
205 establish they will not become invasive but persist at low abundance until either eliminated
206 via ecological drift or increasing opportunistically in response to disturbance. If the trait of an
207 alien species is quite different from those of any resident species (i.e. sitting between red dots
208 in Fig.1a), it is then likely to become either highly invasive (peaks in green zones) or be
209 quickly expelled from the network (valleys in yellow zones), with a 50/50 chance for
210 successful invasion in a species-rich network due to the constraints on any dynamic systems
211 given the continuity of the invasion fitness function (from the Fundamental Theorem of
212 Algebra and the Central Limit Theorem). To this end, the invasibility of the recipient
213 ecological network can be defined as the total width of opportunity niche in the trait space (i.e.
214 the summation of all the green intervals).

215 As an alternative to the static trait approach taken above we could also generate a
216 model community as an adaptive network, where species within the network can co-evolve
217 according to adaptive dynamics (Brännström et al. 2011), or where species with different
218 traits can be continuously introduced into the community from a large species pool (i.e. a
219 meta-community; Gilpin and Hanski 1991; Hubbell 2001). This approach will potentially, but
220 not always, lead to a saturated ecological network (Fig.1b). No alien species can invade a
221 saturated network as the invasion fitness of any introduced species is equal to or less than zero
222 (Fig.1b). These two ways of generating community assemblages sitting either at the
223 equilibrium of ecological dynamics (Fig.1a) or the saturated assembly (Fig.1b) provide an
224 update to the standard naturalisation hypothesis (Duncan and Williams, 2002). Of course,
225 even if the saturated assembly does exist, a community under constant bombardment of IAS

226 intrusion is not likely to be either on the equilibrium or remaining saturated but somewhere
227 between the two extremes. Consequently, we examine how temporal and trait perturbation
228 creates opportunity niche in ecological networks.

229

230 **3. Network invasibility under temporal perturbation**

231 Many factors can drive the change and cyclic fluctuation of resources including land use
232 change, alteration of fire regimes, seasonality and weather conditions. In what follows, we
233 introduce temporal perturbation to a saturated ecological network. Specifically, we examine
234 the fluctuating resource hypothesis (Davis et al. 2000), where fluctuation in resource
235 availability has been identified as the key factor mediating the susceptibility of an ecosystem
236 to invasion by non-resident species. We set a cyclic dynamics to the primary producers
237 (autotrophs in the model; Appendix A) using a sine function to modify resource levels with a
238 particular pulse and magnitude and record the temporal invasion fitness caused by such
239 periodic perturbation in the saturated ecological network.

240 Results confirmed that fluctuating resources can create an opportunity niche with
241 positive invasion fitness when resource levels exceed original levels (Fig.2). The temporal
242 invasiveness of an introduced alien species will reach the maximum when its trait value is
243 optimal for consuming autotrophic resource. The invasibility (length of positive invasion
244 fitness zone along trait axis in Fig.2) appeared high for the first half of the perturbation period
245 (positive phase) and allowed a wide range of introduced species to invade (a long tail towards
246 high trait/trophic direction) but quickly dropped to zero for the second half of the perturbation
247 period (negative phase). This suggests that although perturbation might not create a persistent
248 opportunity niche even for highly invasive alien species in a saturated community,
249 environmental stochasticity can markedly increase the network invasibility in otherwise
250 resistant assemblages.

251 Importantly, rapid resource increase (approaching the 1.0 perturbation period in Fig.2),
252 created an opportunity niche for invasion especially for species with optimal traits for
253 resource consumption, even though resource availability was still below the pre-perturbation
254 levels. Similarly, rapid resource decline (happening at 0.5 perturbation period in Fig.2) also
255 eliminated a portion of opportunity niche around the optimal trait. Evidently, the rate and
256 direction of change in resources as well their absolute level can both affect ecological
257 invasibility, with both playing similar roles in influencing network invasibility. This provides
258 an interesting extension to the fluctuating resource hypothesis which posits that variability in
259 resources promotes invasion in plants (Davis et al. 2000). It further echoes predictions of the

260 paradox of enrichment (Rosenzweig 1971) where enhanced resource level can be
261 accompanied by instability in a food chain.

262

263 **4. Network structure and stability**

264 To simulate an unsaturated ecological network, we randomly altered the trait of heterotrophic
265 species in a saturated network, by an increment following a normal distribution with zero
266 mean and a particular standard deviation (in this case, $\sigma = 0.3$). Theoretically, we can then
267 calculate the Jacobian for randomly-altered networks, with $a_{ij} = \partial(dn_j/dt)/\partial n_i$, defined at the
268 population equilibriums. However, this is impossible in practice; instead, interaction strength
269 is often measured as the observed rate of species j interacting with species i , $a_{ij} = P_{ij}n_in_j$,
270 where P_{ij} measures the per-capita interaction strength. Consequently, we calculated three
271 network structures for 1000 randomly altered networks depicted by the matrix of observed
272 interaction strengths. As these altered networks were generated from the same saturated
273 assembly, they were of the same network size.

274 Metrics of network architecture are diverse. Essentially, these metrics describe
275 different aspects of network structure based on the matrix of interaction strength. These
276 metrics can be divided into two categories: those portraying the role of particular species in
277 the network (e.g. centrality) and those portraying the structure of entire networks. As
278 invasibility is related to the latter, we chose three metrics from this category that depict the
279 three most important features of a matrix – its matrix sparsity, asymmetry and symmetry. In
280 particular, these features are normally measured by three widely used metrics for quantitative
281 networks: connectance, nestedness and modularity. The quantitative connectance metric was
282 computed as the quantitative linkage density divided by the number of species in the network
283 (Tylianakis et al. 2007). A highly connected network is formed largely by generalists with
284 strong and evenly distributed interactions, whereas a less connected network is formed by
285 specialists. We used the metric WINE (weighted interaction nestedness estimator) to quantify
286 the level of nestedness (Galeano et al. 2009). Nested communities are often formed when both
287 specialist and generalist species are present, and where specialists primarily interact with a
288 subset of the partners of generalists. Finally, the level of modularity was measured using a
289 new algorithm *QuanBimo* (Dormann and Strauß 2014; adapted from Clausen et al. 2008). A
290 community with high modularity is compartmentalised into multiple species modules or
291 motifs, with species within the same module interacting strongly with each other but not with
292 species from other modules. All these network metric measurements were implemented in the
293 R library *bipartite* v2.05 (Dormann et al. 2008).

294 We examine how network metrics are associated with the invasibility (the total width
295 of opportunity niche) and the maximum invasiveness (height of the peak invasion fitness).
296 How the system is altered/deviated from its saturated assembly is depicted by the absolute
297 deviation of traits from the traits of the saturated assembly (hereafter, distance to assembly
298 saturation). The asymptotic instability of a system can be measured by the leading eigenvalue
299 of its interaction matrix. When the leading eigenvalue is less than zero, the system will return
300 to its local equilibrium after small perturbations; otherwise, the fluctuations in population
301 abundance will be amplified.

302 As illustrated in Fig.3, there is a strong positive correlation between invasibility and
303 maximum invasiveness (Pearson's $r = 0.418$, $p < 0.001$), suggesting an invasive species often
304 performing more invasively in highly invadable ecosystems. Invasibility showed a positive
305 correlation to the distance to assembly saturation ($r = 0.106$, $p = 0.0005$). In contrast,
306 invasibility showed a negative correlation to ecological stability measured by the lead
307 eigenvalue ($r = -0.267$, $p < 0.0001$). Evidently, since distance to assembly saturation and
308 asymptotic stability reflect different aspects of interaction networks, they have different
309 implications for understanding network function. Such an opposing relationship between the
310 distance to assembly saturation and asymptotic stability is also evident in literature. For
311 instance, Allesina and Tang (2012) reconfirmed that asymptotic stability is negatively
312 affected by nestedness in bipartite mutualistic networks, and as such at ecological time scales,
313 an ecosystem dominated by mutualistic interactions is likely unstable and species poor. In
314 contrast, mutualistic communities can maximise structural stability through potentially
315 enhanced nestedness (Rohr et al. 2014); that is, at long-term time scales, mutualistic
316 interactions can act as a stabilizing force and restrict diversification (Raimundo et al. 2014).
317 Invasibility also shows strong positive correlations ($p < 0.0001$) with all three measurements
318 of network architecture (with quantitative connectance, $r = 0.266$; with nestedness, $r = 0.179$;
319 with modularity, $r = 0.324$). When invasibility is unknown, we could predict it from
320 asymptotic stability and the three measurable network architectures. A generalized linear
321 model of the generated data showed that connectance and modularity are two strong
322 predictors, with predicted invasibility from only these two network structures showing a
323 strong correlation with observed ones ($r = 0.325$, $p < 0.0001$).

324 Although these results only reflect non-causal correlations between network
325 architectures and invasibility, we could still contemplate the following ecological
326 explanations for these positive correlations. First, May (1974) devised a necessary condition,
327 further generalised by Allesina and Tang (2012), to ensure the stability in a complex network,

328 $\alpha(SC)^{1/2} < \beta$, where α stands for the standard deviation of interaction strength, S species
329 richness, C connectance and β self-regulating force (e.g. negative density dependence). It
330 suggests that the stability of a network requires stronger self-regulating force (large β) than
331 potential reinforcing feedbacks from interspecific interactions, captured by the left side of the
332 inequality. A highly connected network (large C) could encompass more reinforcing
333 feedbacks between species, violating this condition and thus rendering network instability.
334 Unstable networks, either due to reinforcing feedbacks or disturbance, could create
335 opportunity niches for invasion, thus augmenting invasibility. Second, a highly nested
336 network suggests a strong hierarchy and asymmetry, potentially from sorting species through
337 multiple ecological filters, with the most extreme specialists only interacting with the most
338 extreme generalists. This asymmetry could potentially create unbalanced energy/material flow
339 from specialists to generalists, creating opportunity niches for introduced specialists that can
340 exploit, perhaps more efficiently than resident generalists, the resident specialists. That is,
341 network asymmetry creates opportunity niches for specialists and thus enhances invasibility.
342 However, as the correlation between nestedness and invasibility is weak, further
343 investigations are needed, especially for different types of ecological networks. Finally, a
344 highly compartmentalized network is formed by clearly bounded modules, with species
345 between modules rarely interacting. This suggests that these modules could have spatially or
346 temporally partitioned available niches and habitats. This nevertheless provides opportunities
347 for the invaders that can explore two or more modules. Species possessing traits with high
348 plasticity or tolerance, and those with complex life cycles (through ontogenetic niche shift),
349 could invade highly compartmentalized networks.

350

351 **5. Invasibility assessment**

352 The above demonstration with the trait-based assembly model suggests that to be capable of
353 directly assessing the invasibility of a recipient ecosystem we need to rely on a
354 comprehensive picture of functional traits that affect biotic interaction strengths and thus
355 population dynamics, as well as overall densities. In practice, however, sufficient data are
356 rarely available for estimating invasibility directly, even when global monitoring and web-
357 based data sharing are actively seeking to make full records of species densities and traits in
358 prioritised ecosystems available. For a rapid assessment of invasibility, we need an indirect or
359 alternative way of capturing the interaction matrix. As shown above, an effective and
360 conceptually and logistically tractable approach is to construct the interaction matrix of the
361 recipient ecosystem (Fig.4a, top). In the absence of a quantitative matrix, a qualitative matrix

362 would suffice. Conservation agencies could work with local experts to compile a semi-
363 quantitative interaction matrix (Fig.4a, middle) with weak interactions indicated by strength
364 0.1, intermediate interactions by 1, and strong interactions by 10. In cases where data were
365 even scarcer, a binary interaction matrix can be used (Fig.4a, bottom). While accurate
366 interaction strengths make enhance predictive power, qualitative matrices are largely
367 sufficient to understand network behaviours. That said, incorrect designation of the
368 directionality of interactions (+, - or 0) may strongly bias the assessment of stability (Quirk
369 and Ruppert, 1965; May, 1973; Jeffries, 1974). Ideally, the matrix should reflect the full
370 species list of the recipient ecosystem. This can also be relaxed by only considering the
371 potential networks that an introduced species will likely to impact or interact with, referred to
372 here as an invader-centric ecological network.

373 Using an estimated interaction matrix at three different levels of acuity (quantitative,
374 semi-quantitative and binary) we infer and compare invasibility from network architecture we
375 use the well-studied biocontrol agent *cum* invader, the Harlequin ladybird, *Harmonia axyridis*
376 (Pallas) (Coleoptera: Coccinellidae) which is predicted to be a major threat to other species
377 within the aphidophagous guild (Roy et al. 2016). Native to Asia, *H. axyridis* has been
378 introduced to many countries around the world as a biocontrol agent of aphids but it has
379 spread to countries in which it was not intentionally introduced. It is now widespread and
380 abundant in many regions and many habitats (Roy et al. 2016). Here, we compare the
381 invasibility of two recipient habitats (agricultural and boreal systems in Europe; see Fig. 4b)
382 to the invasion of *H. axyridis*. Many studies have demonstrated the potential interactions
383 between *H. axyridis* and other aphidophagous species through laboratory and, to a lesser
384 extent, field studies (Pell et al. 2008; Hautier et al. 2011; Brown et al. 2015; Roy et al. 2016).
385 *Harmonia axyridis* engages in intraguild interactions with many species, including other
386 aphid predators such as other ladybirds (Ware et al. 2009), lacewings (Santi and Maini 2006),
387 and hoverflies (Ingels et al. 2015), as well as aphid parasitoids (Chacón et al. 2008) and
388 aphid-pathogenic fungi (Roy et al. 2008). In general these interactions favour *H. axyridis*,
389 though interaction strength and even direction can be influenced by the life stage of the
390 interacting species (Felix and Soares 2004) and the environment (Gardiner et al. 2009).

391 Based on literature and expert opinions, we compiled the semi-quantitative interaction
392 matrices of the European agricultural and boreal systems that are currently being invaded by
393 *H. axyridis* (Fig. 4c and d). The lead eigenvalue before the invasion (removing the entries
394 related to *H. axyridis* in the matrix) is effectively zero for both the agricultural system and
395 boreal forests (absolute value less than 10^{-17}), suggesting that both systems are at weak

396 ecological equilibriums (asymptotically stable). After invasion by *H. axyridis*, both systems
397 become ecologically unstable, with the boreal forests more unstable than the agricultural
398 system (lead eigenvalue: 5.51 vs. 4.12), suggesting a stronger impact of *H. axyridis* on the
399 boreal forests from the perspective of stability.

400 To calculate the three network structures, we replaced all negative entries with zeros
401 as the calculation of these network metrics would otherwise report errors (note, for a
402 predation interaction between species *i* and *j*; if $a_{ij} > 0$, we could either record $a_{ji} < 0$ which is
403 the convention or $a_{ji} = 0$ which is the format for typical network analysis [used here];
404 Newman 2010). Prior to the invasion of *H. axyridis* in our estimated networks, the
405 agricultural system has slightly higher connectance than the boreal system (0.38 vs. 0.34), as
406 well as low modularity (<0.01) and a high level of nestedness (>0.97). After the invasion,
407 connectance dropped slightly in both habitats (0.35 vs. 0.32) while modularity remained low
408 (<0.01) and the nestedness high (~ 1) in both.

409 Comparing these results with general expectations from our models, specifically the
410 lead eigenvalue and connectance (Fig.3), the following interpretations can be proffered. First,
411 before the invasion of *H. axyridis*, the agricultural system is more invadable than the boreal
412 forest. As such, the invasion of *H. axyridis* would be more likely to happen first in the
413 agricultural system. Second, after the invasion of *H. axyridis*, invasibility of both systems was
414 reduced (reducing the risk of future invasion by similar invaders) although the agricultural
415 system is still quite open for future invasions. The impact of the invasion of *H. axyridis* is
416 more strongly felt by the boreal forest with its stability more disturbed (experiencing greater
417 changes in the relative and absolute abundances of species after the arrival of *H. axyridis*). It
418 is worth noting that the above exercise can be easily done before any invasions; a quick
419 picture of the invasibility and the potential impact of the invasion quickly drawn and the
420 invasibility between different habitats and ecosystems fairly compared. This can be
421 accomplished using expert opinions, though the quality of the predictions is of course
422 dependent on ecological realism in the interaction matrix.

423

424 **6. Conclusions**

425 We have demonstrated that ecological networks provide a good model for capturing the
426 complexity of recipient ecosystems, and that the invasiveness of potential invaders and the
427 invasibility of the recipient ecological networks can be defined using the concepts of invasion
428 fitness and assembly saturation as a reference points. In this framework, invasiveness of a
429 potential invader is defined as its invasion fitness (= per-capita population growth rate when

430 the propagule size is trivial) and the invasibility of the network is defined as the width of
431 opportunity niche available for potential invasions. This method is robust to the use of
432 simplified interaction matrices for rapid assessments of network invasibility. Importantly, we
433 argue that invasibility can be inferred from network stability, and that this is more closely
434 linked to assembly saturation than ecological stability. The trait-based approach allowed for
435 the testing of the fluctuating resource hypothesis, thus emphasizing its heuristic value.

436

437 **Acknowledgments**

438 This paper had its origin at a workshop on “Drivers, impacts, mechanisms and adaptation in
439 insect invasions” hosted by the DST-NRF Centre of Excellence for Invasion Biology in
440 Stellenbosch, South Africa, in November 2014. We are grateful to participants at this
441 workshop and to Marc Kenis, Wolfgang Rabitsch, Michael Pocock, Ulf Dieckmann and Åke
442 Brännström for discussions on the concepts presented in this paper. CH is supported by the
443 South African Research Chair Initiative (SARChI), the National Research Foundation of
444 South Africa (grant nos. 81825 and 76912), and the Australian Research Council (Discovery
445 Project DP150103017). HOM receives a PhD Scholarship from the German Academic
446 Exchange Service (DAAD). HER receives co-funding from the Natural Environment
447 Research Council (NERC) and the Joint Nature Conservation Committee (JNCC). HER also
448 acknowledges the COST Action TD1209. DMR acknowledges support from the National
449 Research Foundation of South Africa (grant 85417).

450

451 **References**

- 452 Abrams PA (1983) The theory of limiting similarity. *Annu Rev Ecol Syst* 14:359–376
- 453 Abrams PA (1998) High competition with low similarity and low competition with high
454 similarity: explorative and apparent competition in consumer-resource systems. *Am*
455 *Nat* 152:114–128
- 456 Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483:205–208
- 457 Bar-Massada A, Kent R, Carmel Y (2014) Environmental heterogeneity affects the location of
458 modelled communities along the niche-neutrality continuum. *Proc R Soc B*
459 281:20133249
- 460 Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant-animal
461 mutualistic networks. *Proc Natl Acad Sci USA* 100 (16):9383–9387

- 462 Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate
463 biodiversity maintenance. *Science* 312: 431–433
- 464 Bastola UM, Fortuna MA, Pascual-Garcia A, Ferrera A, Bascompte J (2009) The architecture
465 of mutualistic networks minimizes competition and increases biodiversity. *Nature*
466 458:1018–1020
- 467 Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z,
468 Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM,
469 Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified
470 classification of alien species based on the magnitude of their environmental impacts.
471 *PLoS Biol* 12:e1001850
- 472 Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU,
473 Richardson DM (2011) A proposed unified framework for biological invasions.
474 *Trends Ecol Evol* 26:333–339
- 475 Brännström A, Loeuille N, Loreau M, Dieckmann U (2011) Emergence and maintenance of
476 biodiversity in an evolutionary food-web model. *Theor Ecol* 4:467–478
- 477 Brose U (2011). Extinctions in complex, size-structured communities. *Basic Appl Ecol*
478 12:557–561
- 479 Brown PMJ, Ingels B, Wheatley A, Rhule EL, De Clercq P, Van Leeuwen T, Thomas A
480 (2015) Intraguild predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) on
481 native insects in Europe: molecular detection from field samples. *Entomol Sci* 18:130–
482 133
- 483 Burgos E, Ceva H, Perazzo RPJ, Devoto M, Medan D, Zimmermann M, Delbue AM (2007)
484 Why nestedness in mutualistic networks? *J Theor Biol* 249:307–313
- 485 Chacón J, Landis D, Heimpel G (2008) Potential for biotic interference of a classical
486 biological control agent of the soybean aphid. *Biol Control* 46:216–225
- 487 Chase JM (2005) Towards a really unified theory for metacommunities. *Funct Ecol* 19:182–
488 186
- 489 Clark JS (2012) The coherence problem with the unified neutral theory of biodiversity.
490 *Trends Ecol Evol* 27:198–202
- 491 Clausen AM, Newman MEJ (2008) Hierarchical structure and the prediction of missing links
492 in networks. *Nature* 453:98–101
- 493 Darwin CR (1859) *On the origin of species*. Murray, London

494 Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a
495 general theory of invasibility. *J Ecol* 88:528–534

496 de Visser S, Freymann B, Olff H (2011) The Serengeti food web: empirical quantification and
497 analysis of topological changes under increasing human impact. *J Anim Ecol* 80:465–
498 475

499 Donohue I et al. (2013). On the dimensionality of ecological stability. *Ecol Lett* 16:421–129

500 Dormann CF, Gruber B, Fruend J (2008) Introducing the bipartite package: Analysing
501 ecological networks. *R news* 8:8–11

502 Dormann CF, Strauß R (2014) A method for detecting modules in quantitative bipartite
503 networks. *Meth Ecol Evol* 5:90–98

504 Drake JA (1990) The mechanics of community assembly and succession. *J Theor Biol*
505 147:213–233

506 Drossel B, Higgs P, McKane A (2001) The influence of predator-prey population dynamics
507 on the long-term evolution of food web structure. *J Theor Biol* 208:91–107

508 Duncan RP, Williams PA (2002) Darwin’s naturalisation hypothesis challenged. *Nature*
509 417:608–309

510 Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food
511 webs: robustness increases with connectance. *Ecol Lett* 5: 558–5657

512 Eklöf A, Ebenman B (2006) Species loss and secondary extinctions in simple and complex
513 model communities. *J Anim Ecol* 75:239–246

514 Estrada E (2007) Topological structural classes of complex networks. *Physical Review E*
515 75:016103

516 Felix S, Soares AO (2004) Intraguild predation between the aphidophagous ladybird beetles
517 *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera : Coccinellidae): the
518 role of body weight. *Eur J Entomol* 101:237–242

519 Fridley JD (2011) Biodiversity as a bulwark against invasion: conceptual threads since Elton.
520 In: Richardson DM (ed), Fifty years of invasion ecology: the legacy of Charles Elton,
521 pp. 121–130 Wiley-Blackwell, Oxford

522 Galeano J, Pastor JM, Iriando JM (2009) Weighted-interaction nestedness estimator (WINE):
523 a new estimator to calculate over frequency matrices. *Environ Model Softw* 24:1342-
524 1346

525 Gardiner M, Landis D, Gratton C, DiFonzo C, O'Neal M, Chacon J, Wayo M, Schmidt N,
526 Mueller E, Heimpel G (2009) Landscape diversity enhances biological control of an
527 introduced crop pest in the north-central USA. *Ecol Appl* 19:143–154

528 Gilpin ME, Hanski IA (1991) *Metapopulation dynamics: empirical and theoretical*
529 *investigations*. Academic Press, London

530 Guimarães PR et al. (2007) Build-up mechanisms determining the topology of mutualistic
531 networks. *J Theor Biol* 249:181–189

532 Hautier L, San Martin G, Callier P, de Biseau JC, Grégoire JC (2011) Alkaloids provide
533 evidence of intraguild predation on native coccinellids by *Harmonia axyridis* in the
534 field. *Biol Invas* 13:1805–1814

535 Holland JN, DeAngelis DL (2010) A consumer–resource approach to the density-dependent
536 population dynamics of mutualism. *Ecology* 91:1286–1295

537 Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton
538 University Press, Princeton

539 Hui C, Minoarivelo HO, Nuwagaba S, Ramanantoanina A (2015) Adaptive diversification in
540 coevolutionary systems. In: Pontarotti P (ed.), *Evolutionary Biology:*
541 *Biodiversification from Genotype to Phenotype*. Springer, Berlin, pp.167-186.

542 Ingels B, Van Hassel P, Van Leeuwen T, De Clercq P (2015) Feeding History Affects
543 Intraguild Interactions between *Harmonia axyridis* (Coleoptera: Coccinellidae) and
544 *Episyrphus balteatus* (Diptera: Syrphidae). *PLoS One* 10:e0128518

545 James A, Pitchford JW, Plank MJ (2012) Disentangling nestedness from models of ecological
546 complexity. *Nature* 487:227–230

547 Jeffries C (1974) Qualitative stability and digraphs in model ecosystems. *Ecology* 55:1415–
548 1419

549 Kiers ET, Palmer TM, Ives AR, Bruno JF, Bronstein JL (2010). Mutualisms in a changing
550 world: An evolutionary perspective. *Ecol Lett* 13:1459–1474

551 Kondoh M (2003) Foraging adaptation and the relationship between food-web complexity
552 and stability. *Science* 299:1388–1391

553 Loeuille N, Loreau M (2005) Evolutionary emergence of size structured food webs. *Proc Natl*
554 *Acad Sci USA* 102:5761–5766

555 Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility.
556 *Ecology* 80:1522–1536

557 Loreau M (2000) Are communities saturated? On the relationship between α , β and γ diversity.
558 *Ecol Lett* 3:73–76

559 MacArthur RH (1972) *Geographical ecology*. Harper & Row, New York

560 May RM (1974) *Stability and complexity in model ecosystems*. Princeton University Press,
561 Princeton

562 McCann KS (2000) The diversity-stability debate. *Nature* 405:228–233

563 McKane AJ (2004) Evolving complex food webs. *Eur Phys J B* 38:287–295

564 Mello MAR et al. (2011) The modularity of seed dispersal: differences in structure and
565 robustness between bat and bird-fruit networks. *Oecologia* 167:131–140

566 Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species
567 extinctions. *Proc R Soc B* 271:2605–2611

568 Minoarivelo HO, Hui C (2015) Trait-mediated interaction leads to structural emergence in
569 mutualistic networks. *Evol Ecol*, in press. DOI:10.1007/s10682-015-9798-z

570 Minoarivelo HO, Hui C, Terblanche JS, Kosakovsky Pond SL, Scheffler K (2014) Detecting
571 phylogenetic signal in mutualistic interaction networks using a Markov process model.
572 *Oikos* 123:1250–1260

573 Moravcová L, Pyšek P, Jarošík V, Pergl J (2015) Getting the right traits: reproductive and
574 dispersal characteristics predict the invasiveness of herbaceous plant species. *PLoS*
575 *One* 10:e0123634

576 Morton D, Law R (1997) Regional species pools and the assembly of local ecological
577 communities. *J Theor Biol* 187:321–331

578 Newman MEJ (2006) Modularity and community structure in networks. *Proc Natl Acad Sci*
579 *USA* 103:8577–8582

580 Newman MEJ (2010) *Networks: an introduction*. Oxford University Press, Oxford.

581 Nuwagaba S, Zhang F, Hui C (2015) A hybrid behavioural rule of adaptation and drift
582 explains the emergent architecture of antagonistic networks. *Proc R Soc B* 282:
583 20150320

584 Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination
585 networks. *Proc Nat Acad Sci* 104:19891–19896

586 Olesen JM, Jordano P (2002) Geographic patterns in plant-pollinator mutualistic networks.
587 *Ecology* 89:2416–2424

- 588 Parker GA, Maynard Smith J (1990) Optimality theory in evolutionary biology. *Nature*
589 348:27–33
- 590 Peacock L, Worner SP (2008) Biological and ecological traits that assist establishment of
591 alien invasive species. *NZ Plant Prot* 61:1–7
- 592 Pell JK, Baverstock J, Roy HE, Ware RL, Majerus MEN (2008) Intraguild predation
593 involving *Harmonia axyridis*: a review of current knowledge and future perspectives.
594 *BioControl* 53:147–168
- 595 Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. *Nature* 275:542–544
- 596 Poisot T (2013) An a posteriori measure of network modularity. *F1000 Research* 2:130 (doi:
597 10.12688/f1000research.2-130.v3)
- 598 Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: Where do
599 we stand? In: Nentwig W (ed), *Biological Invasions*, pp. 97–125. *Ecological Studies*
600 193. Springer, Berlin
- 601 Quirk J, Ruppert R (1965) Qualitative economics and the stability of equilibrium. *Rev Econ*
602 *Stud* 32:311–326
- 603 Raimundo RLG, Gibert JP, Hembry DH, Guimarães Jr PR (2014) Conflicting selection in the
604 course of adaptive diversification: the interplay between mutualism and intraspecific
605 competition. *Am Nat* 183:363–375
- 606 Rezende EL, Lavabre JE, Guimaraes Jr PR, Jordano P, Bascompte J (2007) Non-random
607 coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925–
608 928
- 609 Richardson DM, Pyšek P (2006) Plant invasions – merging the concepts of species
610 invasiveness and community invasibility. *Prog Phys Geog* 30:409–431
- 611 Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of
612 biogeographical patterns. *New Phytol* 196:383–396
- 613 Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems.
614 *Science* 345:1253497
- 615 Rosenzweig, M (1971) The paradox of enrichment. *Science* 171:385–387
- 616 Rosindell J, Hubbell SP, He F, Harmon LJ, Etienne RS (2012) The case for ecological neutral
617 theory. *Trends Ecol Evol* 27:203–208

- 618 Rossberg AG, Brännström, Å, Dieckmann, U. (2010) How trophic interaction strength
619 depends on traits: a conceptual framework for representing multidimensional trophic
620 niche spaces. *Theor Ecol* 3:13–24
- 621 Roy HE et al. (2016) *Harmonia axyridis*: an inspiration for global collaborations on invasion
622 biology. *Biol Invasions* (in press)
- 623 Roy HE, Baverstock J, Ware R, Clark S, Majerus M, Baverstock K, Pell J (2008) Intraguild
624 predation of the aphid pathogenic fungus *Pandora neoaphidis* by the invasive
625 coccinellid *Harmonia axyridis*. *Ecol Entomol* 33:175–182
- 626 Santi F, Maini S (2006) Predation upon *Adalia bipunctata* and *Harmonia axyridis* eggs by
627 *Chrysoperla carnea* larvae and *Orius laevigatus* adults. *Bull Insectol* 59:53–58
- 628 Shea K, Chesson P (2002) Community ecology theory as a framework for biological
629 invasions. *Trends Ecol Evol* 17:170–176
- 630 Stohlgren TJ, Barnett DT, Kartesz J (2003). The rich get richer: patterns of plant invasions in
631 the United States. *Front Ecol Environ* 1:11–14
- 632 Stouffer DB, Bascompte J (2011) Compartmentalisation increases food-web persistence. *Proc*
633 *Natl Acad Sci USA* 108: 3648–3652
- 634 Suweis S, Simini F, Banavar JR, Maritan A (2013) Emergence of structural and dynamical
635 properties of ecological mutualistic networks. *Nature* 500:449–452
- 636 Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of
637 mutualistic and trophic networks. *Sciences* 329:853–856
- 638 Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of
639 resource competition, invasion, and community assembly. *Proc Natl Acad Sci USA*
640 101:10854–10861
- 641 Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of
642 tropical host-parasitoid food webs. *Nature* 445:202–205
- 643 Vacher C, Piou D, Desprez-Loustau M (2008) Architecture of an antagonistic tree/fungus
644 network: the symmetric influence of past evolutionary history. *PLoS One* 3:e1740
- 645 Valdovinos FS, Ramos-Jiliberto R, Garay-Narvaèz L, Urbani P, Dunne JA (2010)
646 Consequences of adaptive behaviour for the structure and dynamics of foodwebs. *Ecol*
647 *Lett* 13:1546–1559
- 648 van Baalen M, Krivan V, van Rijn PCJ, Sabelis MW (2001) Alternative food, switching
649 predators, and the persistence of predator–prey systems. *Am Nat* 157:512–524

- 650 Ware RL, Yguel B, Majerus MEN (2009) Effects of competition, cannibalism and intra-guild
651 predation on larval development of the European coccinellid *Adalia bipunctata* and
652 the invasive species *Harmonia axyridis*. *Ecol Entomol* 34:12–19
- 653 Waxman D, Gavrillets S (2005) 20 questions on adaptive dynamics. *J Evol Biol* 18:1139–1154
- 654 Yodzis P (1981) The stability of real ecosystems. *Nature* 289:674–676
- 655 Zhang F, Hui C, Terblanche JS (2011) An interaction switch predicts the nested architecture
656 of mutualistic networks. *Ecol Lett* 14:797–803
- 657

658

659 **Figure Legends:**

660 **Fig.1:** Invasion fitness of an introduced species as a function of its trait value relative to the
661 trait values of the resident species in the ecological networks. Red dots indicate the trait
662 values of native resident species. **(a)** A randomly generated network at its ecological
663 equilibrium. Only introduced species with traits lie in the green intervals can establish and
664 invade the recipient ecological network; introduced species with traits lie in the yellow
665 intervals will be repelled by the network (i.e. wiped out from the resident species/ecosystem).
666 Invasibility is thus defined as the total width of the green intervals along the zero-fitness line.
667 **(b)** A saturated assembly is defined as the recipient network with zero invasibility. Parameter
668 values are the same as in Fig.1 of Brännström et al. (2011).

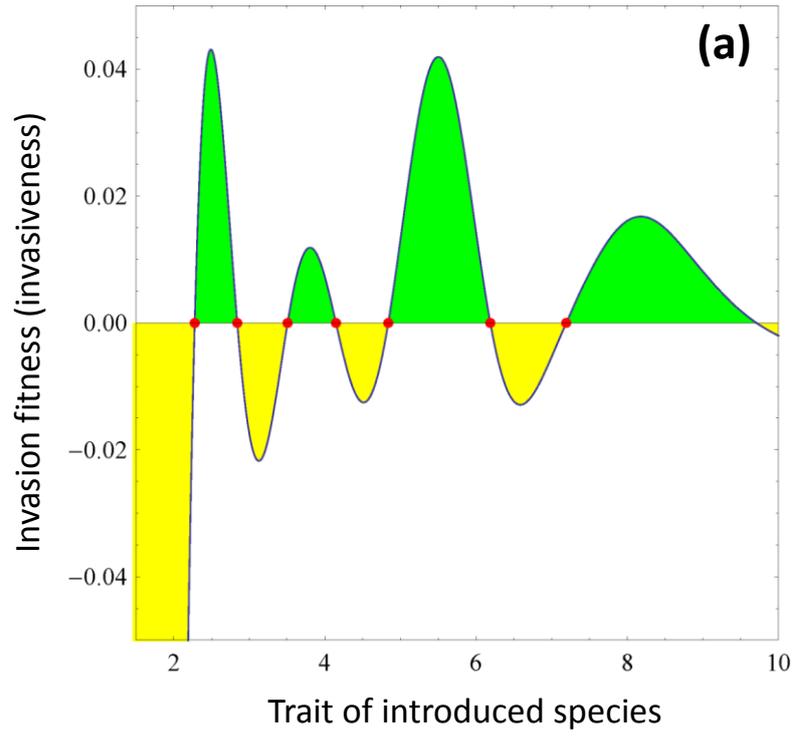
669 **Fig.2:** Invasion fitness of an introduced species as a function of its trait value in an ecological
670 network. The resources of the saturated assembly in Fig.1b, n_0 , are disturbed by adding a
671 periodic perturbation (sine form with pulse 10 and magnitude 100). An alien species with the
672 trait and timing of introduction in the positive invasion fitness zone can invade the ecological
673 network; otherwise it will be repelled from the network. The peak of positive invasion fitness
674 corresponds to the first quarter of the period and the optimal trait for resource consumption (r
675 $= \mu = 2$).

676 **Fig.3:** Relationships between invasibility, maximum invasiveness, distance to assembly
677 saturation (DAS) and the lead eigenvalue of the interaction matrix, as well as network
678 architectures (quantitative connectance, levels of nestedness and modularity) in 1000 random
679 ecological networks around the saturated assembly. Block tone corresponds to the frequency
680 of networks.

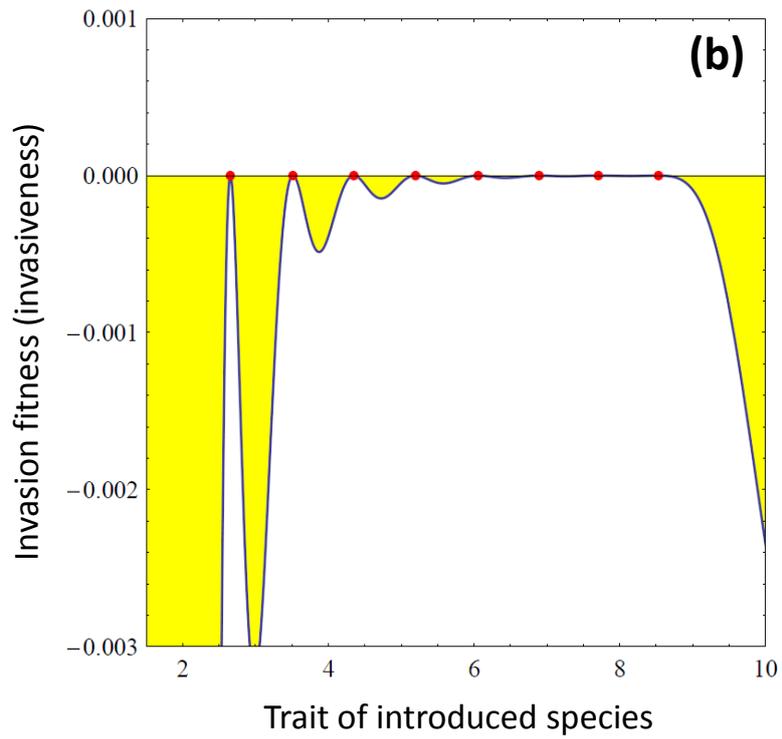
681 **Fig.4:** Interaction matrices in practice. (a) An illustration of quantitative, semi-quantitative
682 and qualitative interaction matrices (top, middle and bottom), with decreasing demands for
683 data quality. (b) A picture of one European agricultural system with boreal habitat in
684 background (Photo: H.E. Roy); both invaded by invasive alien ladybird *Harmonia axyridis*.
685 Panels (c) and (d) are semi-quantitative interaction matrices for agricultural and boreal
686 systems in Europe, based on literature and expert opinion. Acronyms: HA: *Harmonia axyridis*;
687 AB: *Adalia bipunctata*; CS: *Coccinella septempunctata*; CC: *Chrysoperla carnea*; EB:
688 *Episyrphus balteatus*; PN: *Pandora neoaphidis*; DC: *Dinocampus coccinellae*; AD: *Adalia*
689 *decempunctata*; HS: *Halyzia sedecimguttata*; PF: Phorid fly; AP: aphids.

690

691 **Fig.1:**



692



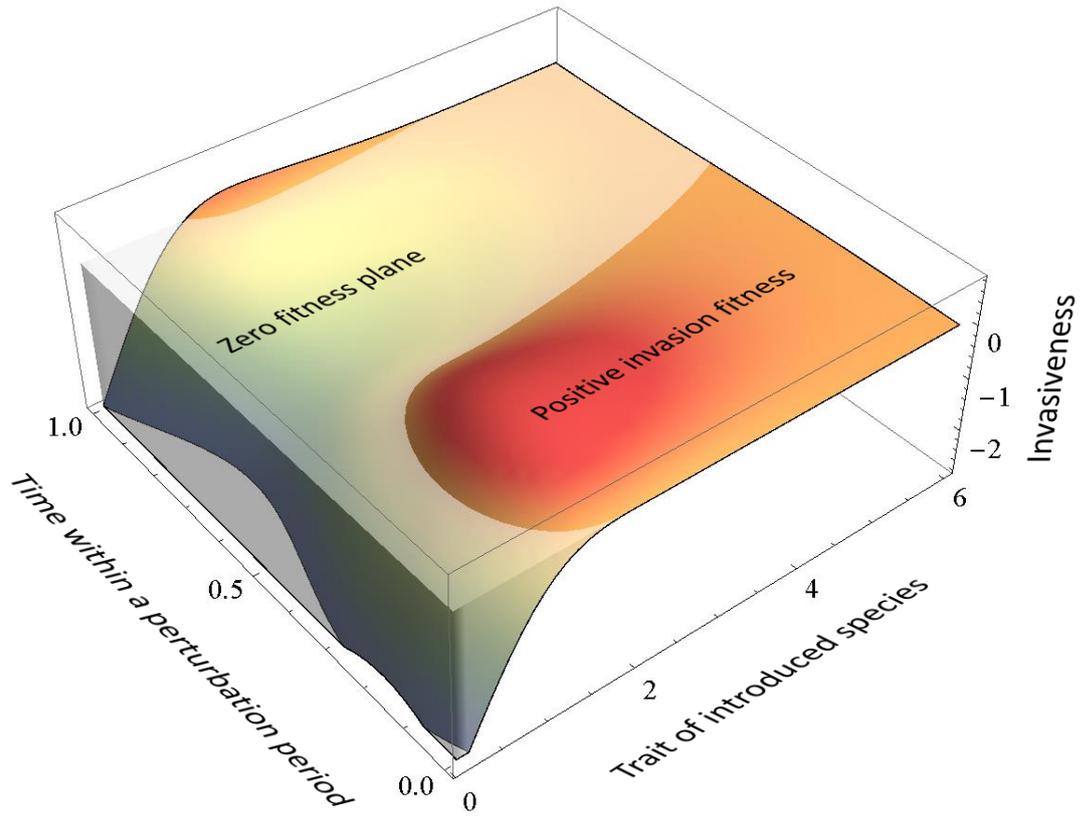
693

694

695

696

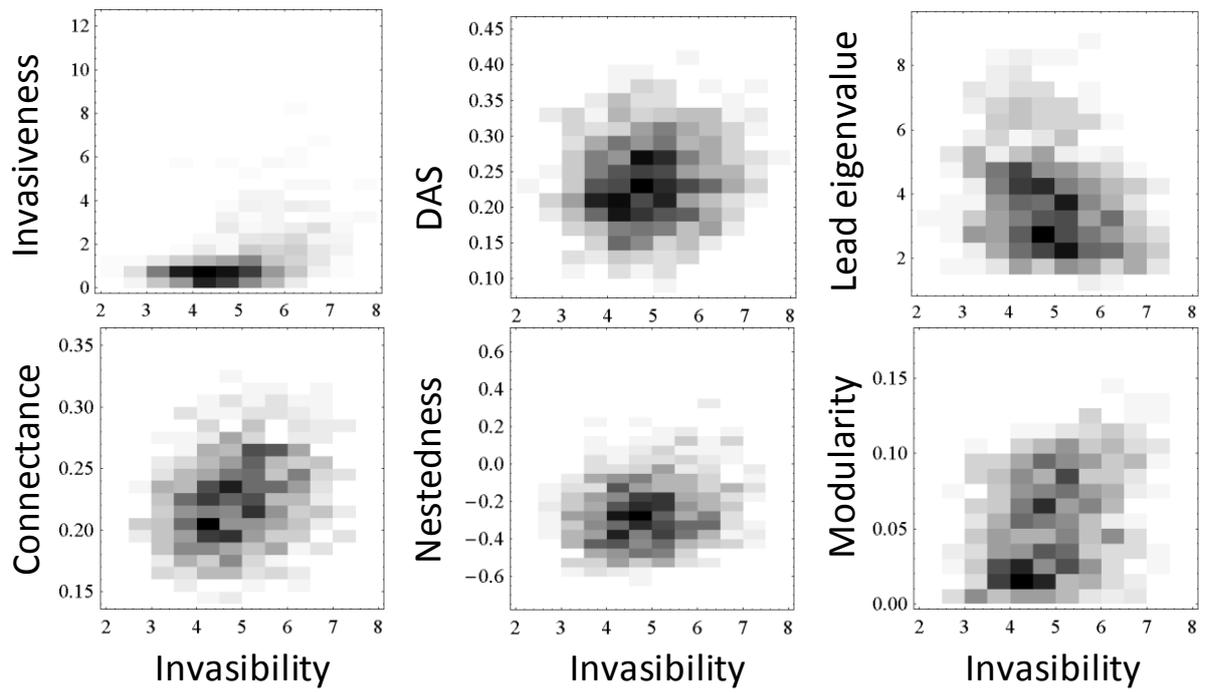
697 **Fig.2:**



698

699 **Fig.3:**

700



701

702

(a)

	spp1	spp2	spp3	spp4	spp5
spp1	-0.96	-0.44	-0.11	0.58	-0.35
spp2	0.33	0.58	0.65	-0.13	-0.85
spp3	-0.23	-0.98	-0.24	-0.37	0.45
spp4	0.64	-0.44	0.36	-0.01	-0.43
spp5	-0.03	-0.46	0.40	-0.19	0.62

spp1	-10	-1	-0.1	1	-1
spp2	0.1	1	1	-0.1	-10
spp3	-0.1	-10	-0.1	-1	1
spp4	1	-1	1	-0.1	-1
spp5	-0.1	-0.1	1	-0.1	1

spp1	-1	-1	0	1	-1
spp2	0	1	1	0	-1
spp3	0	-1	0	-1	1
spp4	1	-1	1	0	-1
spp5	0	-1	1	0	1



(c)

	HA	AB	CS	CC	EB	PN	DC	AP
HA	-1	0	-0.1	-0.1	0	0	-0.1	10
AB	-10	-0.1	-0.1	-0.1	0	0	-0.1	10
CS	-0.1	0	-1	-0.1	0	0	-1	10
CC	-10	0	0	-0.1	0	0	0	10
EB	-10	0	0	-0.1	0	0	0	10
PN	0.1	0.1	0.1	0	0	0	0	10
DC	0	0	0	0	0	0	-0.1	0
AP	-10	-10	-10	-10	-10	-10	0	0

(d)

	HA	AB	AD	HS	CC	EB	PN	DC	PF	AP
HA	-1	0	0	0	-0.1	0	0	-0.1	-0.1	10
AB	-10	-0.1	0	0	-0.1	0	0	-0.1	-1	10
AD	-10	0	-0.1	0	-0.1	0	0	-0.1	-1	10
HS	-10	0	0	0	-0.1	0	0	-0.1	0	0.1
CC	-10	0	0	0	-0.1	0	0	0	0	10
EB	-10	0	0	0	0	0	0	0	0	10
PN	0.1	0.1	0.1	0	0	0	0	0	0	10
DC	0	0	0	0	0	0	0	-0.1	0	0
PF	-0.1	0	0	0	-0.1	0	0	-0.1	0	0
AP	-10	-10	-10	0	-10	-10	-10	0	0	0

704

705

706 **Online Appendix:**

707 Appendix A: A trait-based assembly model.

708 We consider a generalised version of the Loeuille and Loreau (2005) model developed by
709 Brännström et al. (2011) which depicts the *per capita population change rate* as a function of
710 population growth derived from prey consumption minus mortality from senescence,
711 predation and interference competition:

$$712 \quad \frac{1}{n_i} \frac{dn_i}{dt} = \lambda \sum_{j=0}^s \frac{P_{ji} n_j}{\exp(\Delta r_{ij})} - \left(D_i + \sum_{j=1}^s P_{ij} n_j \right) - \sum_{j=1}^s C_{ij} n_j$$

713 where λ is the conversion efficiency for the consumptive interactions. The per-capita
714 predation rate of species i preying on species j is set to be trait-mediated, $P_{ji} = \gamma_0 N(\Delta r_{ij} - \mu, \sigma_\gamma)$,
715 where $N(a, b)$ is the probability density function of normal distribution with mean a and
716 standard deviation b , Δr_{ij} the trait difference of species i and j , $r_i - r_j$ (considering the logarithm
717 of body size relative to that of the autotroph). The coefficients μ and σ_γ represent the optimal
718 trait ratio of predator to prey and the dietary breadth of the predator. The natural mortality is
719 also assumed to be trait-mediated, $D_i = d_0 \exp(-r_i/4)$ (Peters, 1983). The intensity of
720 interference competition is at its maximum when the two competing species have identical
721 traits, $C_{ij} = k_0 N(\Delta r_{ij}, \sigma_k)$. In addition, the dynamics of the autotroph (resource base) is
722 governed by, $dn_0/dt = n_0(g - k_0 n_0 - \sum_{j=1}^s P_{0j} n_j)$, where g is the intrinsic population growth rate
723 (see detail model description in Brännström et al. 2011). The resources n_0 are disturbed by
724 adding a periodic perturbation (sine form with pulse 10 and magnitude 100).

725

726

727