Defining invasiveness and invasibility in ecological networks

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Abstract

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

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

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1. Introduction

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

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

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

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

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

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2. Invasion fitness

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

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

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

3. Network invasibility under temporal perturbation

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

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

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

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 Strauβ 2014; adapted from Claused 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

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

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

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657

Figure Legends:

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

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

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

Fig.4: Interaction matrices in practice. (a) An illustration of quantitative, semi-quantitative and qualitative interaction matrices (top, middle and bottom), with decreasing demands for data quality. (b) A picture of one European agricultural system with boreal habitat in background (Photo: H.E. Roy); both invaded by invasive alien ladybird *Harmonia axyridis*. Panels (c) and (d) are semi-quantitative interaction matrices for agricultural and boreal systems in Europe, based on literature and expert opinion. Acronyms: HA: *Harmonia axyridis*; AB: *Adalia bipunctata*; CS: *Coccinella septempunctata*; CC: *Chrysoperla carnea*; EB: *Episyrphus balteatus*; PN: *Pandora neoaphidis*; DC: *Dinocampus coccinellae*; AD: *Adalia decempunctata*; HS: *Halyzia sedecimguttata*; PF: Phorid fly; AP: aphids.
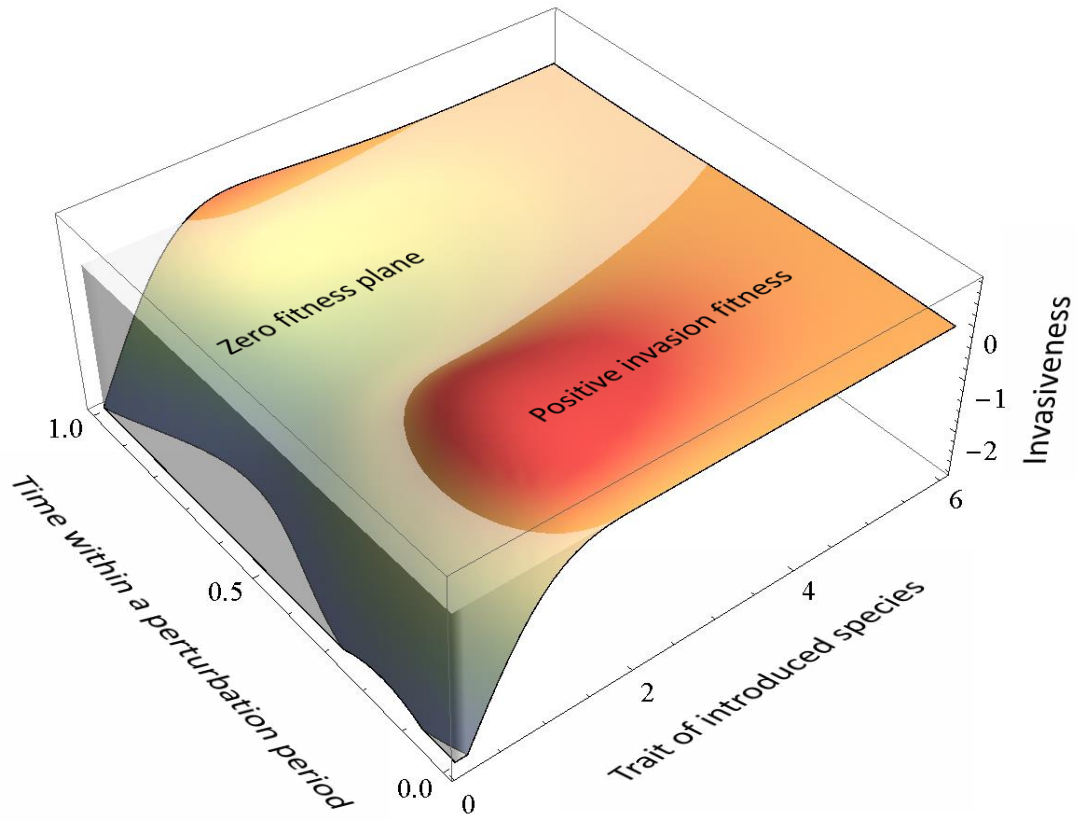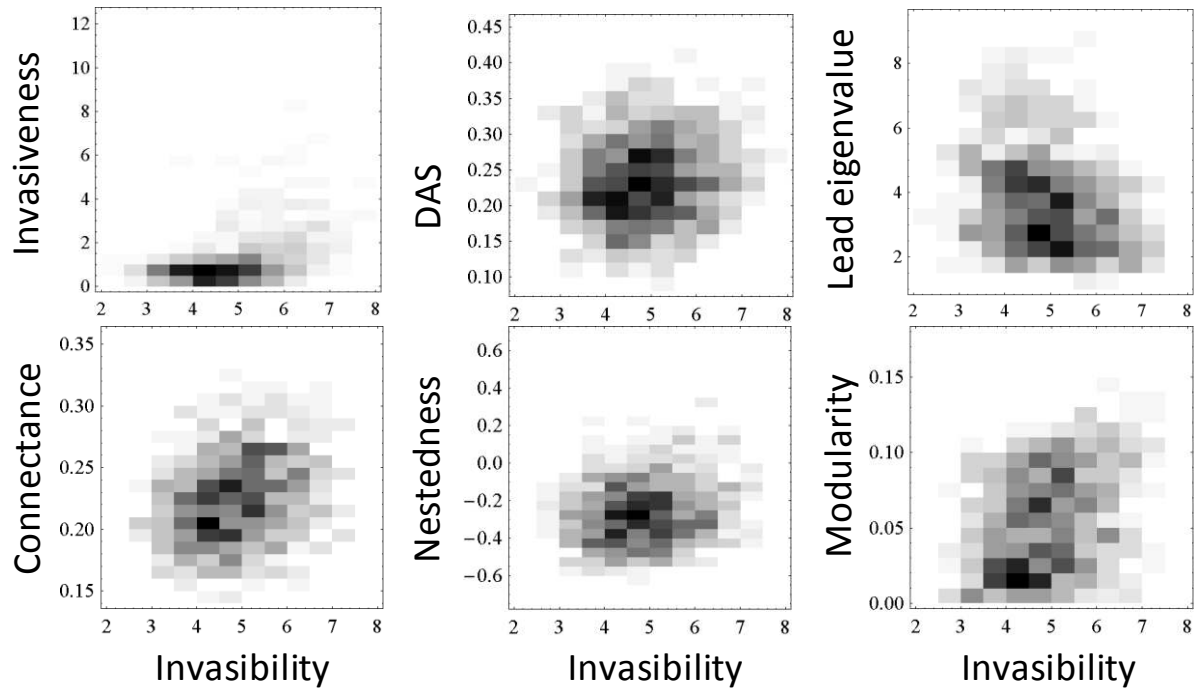
Fig.1:
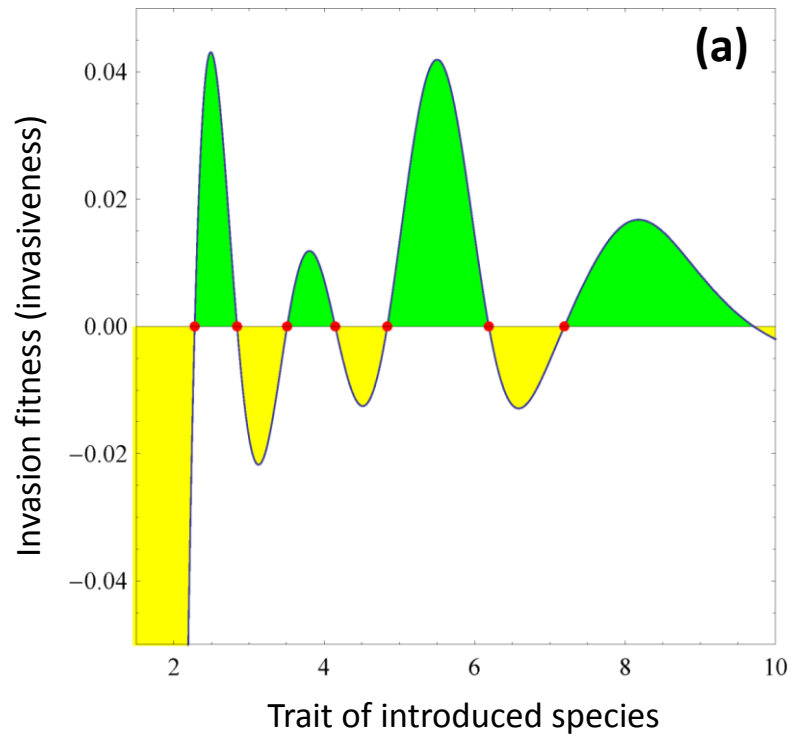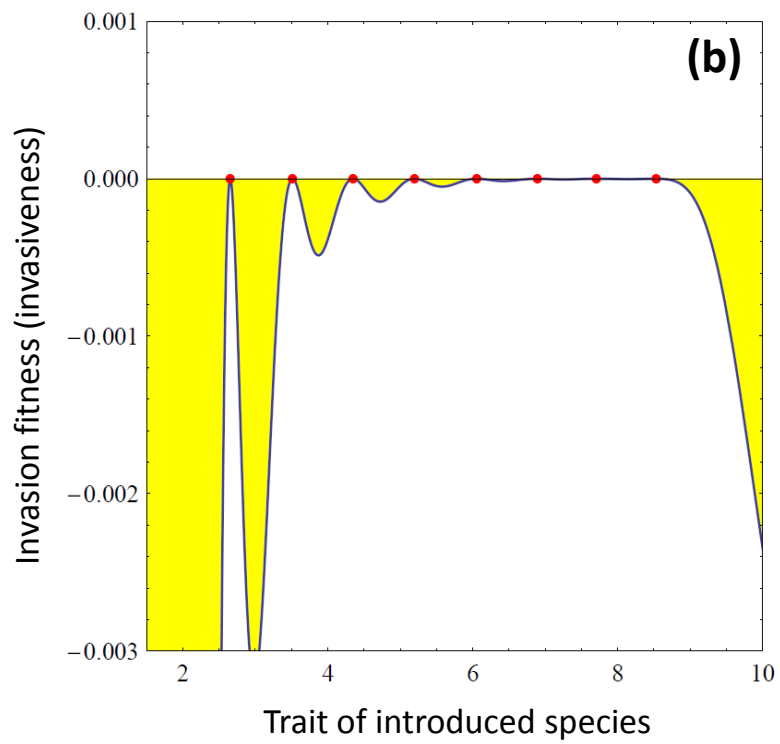
Fig.2:

699 **Fig.3:**

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701

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Fig.4:

(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

(b)

(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

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

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

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727