

Abstract

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Ecological networks that exhibit stable dynamics should theoretically persist longer than those that fluctuate wildly. Thus, network structures which are over-represented in natural systems are often hypothesised to be either a cause or consequence of ecological stability. Rarely considered, however, is that these network structures can also be by-products of the processes that determine how new species attempt to join the community. Using a simulation approach in tandem with key results from random matrix theory, we illustrate how historical assembly mechanisms alter the structure of ecological networks. We demonstrate that different community assembly scenarios can lead to the emergence of structures that are often interpreted as evidence of ‘selection for stability’. However, by controlling for the underlying selection pressures, we show that these assembly artefacts—or spandrels—are completely unrelated to stability or selection, and are instead by-products of how new species are introduced into the system. We propose that these network-assembly spandrels are critically overlooked aspects of network theory and stability analysis, and we illustrate how a failure to adequately account for historical assembly can lead to incorrect inference about the causes and consequences of ecological stability.

Keywords

Coexistence, community assembly, interspecific competition, network structure, stability.

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INTRODUCTION

Ecological networks often exhibit strikingly non-random patterns. A dominant hypothesis is that these networks develop through a selective process that prunes unstable configurations, resulting in patterns that confer robustness and stability (Hofbauer & Sigmund 1988; Proulx *et al.* 2005; Borrelli *et al.* 2015; Saiz *et al.* 2017). Such arguments are often grounded in our understanding of community dynamics (Borrelli 2015): ecological networks that exhibit wild fluctuations should be less likely to persist through time because of stochastic extinctions, such that we should tend to see network patterns that lead to more controlled dynamics. Yet an alternative possibility is that these patterns are ‘artefacts of assembly’ that arise due to specific constraints on the system, having no inherent connection to network dynamics or stability (Gould & Lewontin 1979; Barrett & Hoekstra 2011; Valverde *et al.* 2017). Despite enormous interest in understanding the links between ecological network structure and dynamics (Suweis *et al.* 2013; Rohr *et al.* 2014; Allesina *et al.* 2015; Barabás *et al.* 2016), we still have little knowledge of how community assembly shapes ecological networks.

The assembly of a biological system is broadly dictated by the interplay between two forces: the processes that determine how, when and why new variation is introduced into the system, and the selective mechanisms that determine which new features persist and at what frequencies (Nee 1990). Although selection is a dominant structuring force throughout natural systems, a failure to account for assembly constraints can lead to incorrect inference about the extent or magnitude of selection. For example, in noting that the dominant evolutionary paradigm of the

time overemphasised adaptive forces, Gould & Lewontin (1979) cautioned that some organismal traits may arise as an accidental by-product of the way the system was formed; that is, features can appear to have current utility, yet have no intrinsic adaptive origin. More recently, when discussing why some motifs are over-represented in cellular networks, Solé & Valverde (2006) argued that these non-random patterns might simply reflect ‘underlying rules of construction’ that are erroneously being interpreted as evidence for selection. Inspired by the work of Gould & Lewontin (1979), they dubbed this phenomenon the ‘network spandrel’ hypothesis, a nod to a type of cathedral archway which is often assumed to be an aesthetic choice (i.e. assumed to be ‘selected’ by the architect), but which is in fact a necessary aspect of construction.

From an ecological perspective, a ‘network spandrel’ refers to any network property that emerges as a by-product of how species join the community, and not as a result of selective forces that determine survival and abundance. More rigorously, a spandrel is a feature that *appears* to carry a signal for selection, but which actually arises due to assembly constraints (Gould & Lewontin 1979). Indeed, ecological networks are typified by patterns that seem to indicate underlying selective forces, including a nested organisation of interactions (Bascompte *et al.* 2003; Thébaud & Fontaine 2010), broad degree distributions (Dunne *et al.* 2002) and the preponderance of certain network motifs (Milo *et al.* 2002; Stouffer *et al.* 2012). Because many of these network patterns are linked to stability and robustness (e.g., Prill *et al.* 2005), it is tempting to assume that their over-representation indicates selection for stability (Borrelli 2015), and yet it remains unexplored whether these features might instead be spandrels of assembly.

Disentangling whether an empirical pattern has emerged due to assembly constraints or to selective pruning is challenging, requiring multiple converging lines of experimental, observational and theoretical evidence (Barrett & Hoekstra 2011). Certainly, assembly dynamics can have pronounced effects on the composition of natural communities and the shape of the resulting networks (Kashtan & Alon 2005; Nuismer *et al.* 2013; Fahimipour & Hein 2014; Shtilerman *et al.* 2015; Ponišio & M'Gonigle 2017), but the relative importance of assembly constraints vs. selective mechanisms remains unclear. If a specific feature rarely occurs as a by-product of assembly, then its over-representation in an empirical network is strong evidence of a selective force. Conversely, if a specific feature commonly emerges under a specific assembly rule, then its over-representation provides little insight into the selective pressures operating on the network, but might alternately reveal the historical assembly processes at work (Solé & Valverde 2006). Gaining such understanding will require the merging of concepts, tools and techniques from across community assembly theory and network stability analysis.

Here, we illustrate how assembly history can lead to the over-representation of network patterns that are commonly thought to indicate ‘selection for stability’. First, we use a simple model of interspecific competition to explore how two different assembly processes (immigration vs. adaptive radiation) alter the structure of the resulting network. Then, by taking advantage of results in random matrix theory, we show that communities assembled via immigration yield networks that are indistinguishable from random, whereas communities assembled via adaptive radiation exhibit markedly complex and rich network properties. We demonstrate that these non-random network structures (i.e. spandrels) would appear to indicate ‘selection for stability’, and yet they arise purely as by-products of assembly. Lastly, we add increasing realism to the system by incorporating a model of niche overlap, and we demonstrate that the assembly spandrels are robust to underlying model specifications and choice of network metric. Collectively, our goal is to illustrate how historical assembly mechanisms can alter the structure of empirical networks, and to show that a failure to account for historical assembly processes can lead to incorrect inference about the role of ‘selection for stability’ operating within the network.

ASSEMBLING ECOLOGICAL COMMUNITIES

To demonstrate how community assembly can affect the structure of ecological networks, we use a simple Lotka–Volterra model of interspecific competition to act as the selective force in the community (Post & Pimm 1983; Taylor 1988; Kokkoris *et al.* 1999). Consider a community comprised of n interacting species, and let $\mathbf{x} = (x_1, \dots, x_n)'$ denote the abundance of each species at a specific point during the assembly sequence. The rate of change is modelled as:

$$\frac{dx_i}{dt} = x_i(r_i + \sum_j a_{ij}x_j) \quad \text{for } i = 1, \dots, n, \quad (1)$$

where $\mathbf{r} = (r_1, \dots, r_n)'$ is the vector of intrinsic growth rates, and the a_{ij} are the ‘interaction coefficients’, reflecting the per capita effect of species j on i .

Since our focus is on competition, the a_{ij} are assumed to be negative throughout. Furthermore, in order to ensure that emergent network patterns are a direct result of competitive dynamics—and not otherwise due to ancillary fitness differences among species—we assume, without loss of generality, that species have identical growth rates ($r_i = 1$ for all i) and that intraspecific competitive effects are equivalent across species ($a_{ii} = -1$ for all i) (Kokkoris *et al.* 1999). Thus, species differ only in the magnitude and distribution of their inter-specific interaction coefficients. Lastly, we also restrict our analysis to symmetric competition, such that $a_{ij} = a_{ji}$ for all i, j . This assumption guarantees that any community will converge to its steady-state equilibrium rather than display oscillatory or chaotic dynamics (MacArthur 1970), thereby allowing us to accurately capture long-term dynamics without having to invoke additional assumptions about species’ immigration or mutation rates.

We focus on two different mechanisms of assembly (Fig. 1). First, in the ‘immigration scenario’, new species colonise from outside the community, such that the potential invader has no relationship with the resident species. Second, in the ‘adaptive radiation’ scenario, a species within the community diversifies and splits into two closely related species. Although we use the terms ‘immigration’ and ‘radiation’ to reflect the overarching differences between these two scenarios, it is important to keep in mind that immigration, mutation and speciation are complex processes that vary substantially across systems (MacArthur & Wilson 1967; Lenormand 2002; Gavrilets & Vose 2005; Rundell & Price 2009). Thus, these scenarios are only intended to serve as two simple examples, selected from the multitude of ways that new biological diversity can arise in natural communities (see Supplemental Note).

For both scenarios, the general assembly process is as follows. First, we start with a single species. Then, at each iteration, we: (1) find a new species that can successfully invade the current community; (2) add this species to the system and simulate the long-term dynamics until the community reaches a stable configuration; and (3) repeat, sequentially adding new species and pruning at each step. At each iteration, the introduction of the new species disrupts the current equilibrium; the invader may succeed in joining the community without loss of diversity, or it may lead to an extinction cascade of one or more resident species.

Each potential invader is assigned a set of interaction coefficients dictating how it interacts with the resident species in the community (Fig. 1). Given these interaction coefficients, a_{ij} , the new species i can invade provided that it satisfies the ‘invasion criterion’:

$$r_i + \sum_{j \neq i} a_{ij}x_j > 0. \quad (2)$$

What distinguishes the two scenarios is how we generate these interaction coefficients. In the immigration scenario (Fig. 1, top row), the a_{ij} are first sampled independently from a uniform $\mathcal{U}(-1, 0)$ distribution, with a_{ii} set equal to -1 . If the invasion criterion in eqn 2 is satisfied, then we add the invader to the community; if not, then we randomly select one of the

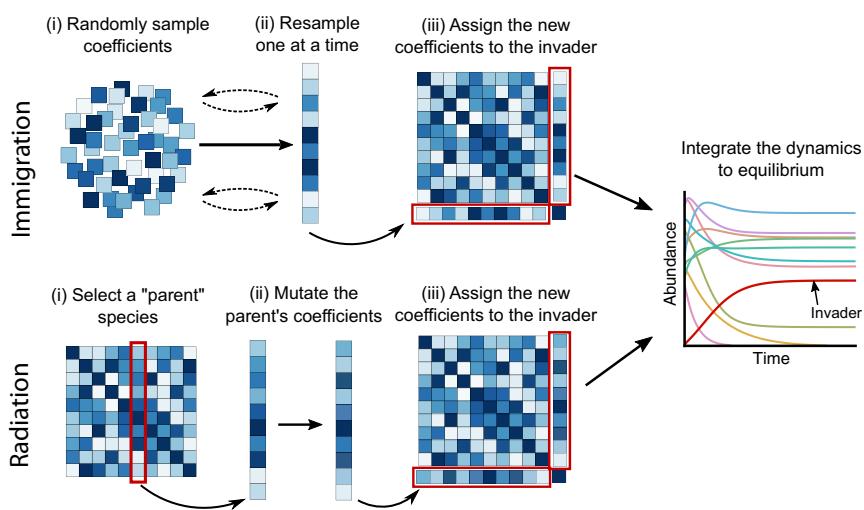


Figure 1 A visual depiction of the two different assembly processes. In the immigration case (top row), interaction coefficients are sampled from a fixed distribution and subsequently assigned to the new invader. Coefficients are then resampled one at a time until the species can successfully invade. In the radiation case (bottom row), a parent species is first selected from among the current species in the community, and the parent's interaction coefficients are perturbed slightly. If the species can invade it is added to the community; if not, the coefficients are discarded and a new parent is selected. In both cases, the dynamics of the system are integrated until the system reaches equilibrium, with some of the species potentially going extinct as a result of the invader. This process is repeated until the community reaches 100 species.

a_{ij} and resample this value from a uniform $\mathcal{U}(-1, 0)$ distribution. If this new value brings the species closer to satisfying the invasion criterion (i.e. closer to being non-negative), we keep this coefficient; if not, we discard it and keep the original value. We then repeat the process, randomly resampling the coefficients one at a time (with replacement), until the invasion criterion is satisfied and the species can invade (see Supplemental Methods).

Under the radiation scenario (Fig. 1, bottom row), we generate new interaction coefficients by first selecting a ‘parent’ from among the resident species in the community. We then perturb the parent’s interaction coefficients by multiplying each by a random value (here, selected from a $\mathcal{U}(0.97, 1.03)$ distribution, or a perturbation of up to 3%), and we bound the perturbed values to within $[-1, 0]$ if needed. If eqn 2 is satisfied, then we add the new species to the community alongside its parent species; if not, we select at random a new parent and once again perturb its interaction coefficients. We repeat this process, each time randomly selecting a new parent (with replacement) and perturbing its coefficients, until the invasion criterion is satisfied and the species can invade.

Once a successful invader is found, we check if the equilibrium of the new community is stable and feasible. These two criteria are investigated by first calculating the equilibrium value for the new community, given by:

$$\mathbf{x}^* = (x_1^*, \dots, x_n^*)' = -A^{-1}\mathbf{r}, \quad (3)$$

where A is the matrix of interaction coefficients, a_{ij} . The feasibility criterion means that all species have positive abundances at equilibrium (i.e. $x_i^* > 0$ for all i), and stability is equivalent to all of the eigenvalues of A being negative (May 1973). If either of these two conditions is not satisfied, then this implies that one or more species will eventually go extinct. If this occurs, then we add the invader to community at a low initial

abundance (set at $x_i = 1 \times 10^{-5}$), and we integrate the dynamics of the community over an arbitrarily large interval. Species whose abundances have shrunk to below a fixed minimum threshold for survival (set at $x_i < 1 \times 10^{-6}$) are discarded, and we recheck stability and feasibility of the updated species assemblage. This process is repeated until the community is pruned to a stable configuration, at which point we introduce a new invader and repeat the process. For all subsequent results, the assembly process is repeated until each community reaches 100 unique species.

Assembly trends

The radiation scenario required an order of magnitude more invasions to reach a similar community size as the immigration scenario (Fig. 2). This slower increase in the radiation scenario is primarily driven by the fact that the invaders are attempting to join a community containing at least one (and typically a small cluster of) similar species. Thus, an invader is more likely to cause one or more nearby species to go extinct—essentially as a result of the theory of limiting similarity (MacArthur & Levins 1967). This creates a ‘two steps forward, one step back’ pattern in community buildup, leading to slower community buildup in the radiation scenario.

It is important to note that these initial results do not imply that real-world communities assembled via immigration will necessarily grow faster than those assembled via radiation, as this would ultimately depend on the rate of immigration or mutation across systems. Because we focus on symmetric competition, all of the feasible and stable communities are guaranteed to converge to their equilibrium state (MacArthur 1970), alleviating the need to invoke additional assumptions about the rate and timing of speciation or immigration (apart from assuming that communities equilibrate relatively rapidly

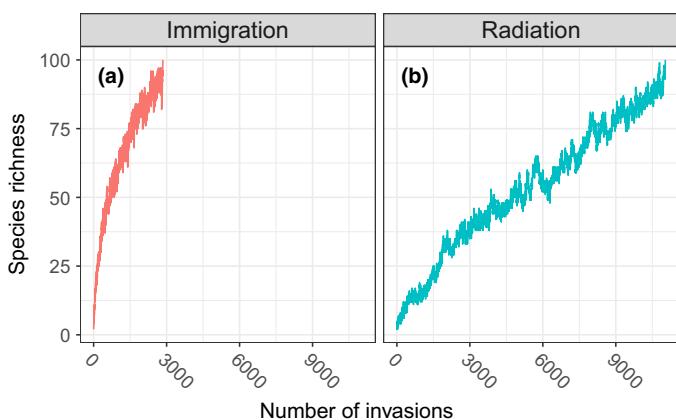


Figure 2 The number of invasions needed to reach 100 species differed substantially between the (a) immigration and (b) adaptive radiation scenarios. In the radiation scenario, species are attempting to invade into a community that typically contains a small cluster of similar species. Thus, in the process of establishing, the invader often causes one or more resident species to go extinct. This leads to a pronounced pattern of community growth and contraction in the radiation scenario relative to the immigration scenario.

compared to speciation or immigration). What these assembly patterns do illustrate, however, is that assembly via radiation can lead to more frequent extinction cascades as a consequence of the invader displacing resident species.

At this point, the traditional approach in community-assembly theory is to analyze assembly trends via ‘mean-field’ analysis, that is, by focusing on aggregate community properties (Post & Pimm 1983; Taylor 1988; Drake 1990; Virgo *et al.* 2006; Powell & McKane 2009). When we follow this approach, we see that the two scenarios exhibit qualitatively and quantitatively similar aggregate trends (Fig. 3). In particular, the mean interaction strength decreases as the community grows, following previous community-assembly models (Kokkoris *et al.* 1999); total species abundance increases; mean abundance decreases; and the variation in interaction strength declines as the selection process ‘evens out’ the community. The largest discrepancy is that the radiation case exhibits significantly lower total abundance (Fig. 3b), once again reflecting the fact that, under radiation, species are invading into a cluster of similar species, forcing them to persist at lower abundances due to intense within-cluster competition.

Nevertheless, apart from these differences in the relative magnitude of the effects, there is no clear fingerprint of assembly on the resulting trends—that is, the patterns are qualitatively identical. These initial results reinforce the fact that the same selection forces are being applied to both communities, leading to similar overall assembly dynamics. From the perspective of community-assembly patterns, there is thus little evidence for assembly spandrels. However, these mean-field patterns are only coarse approximations of community network structure.

Network structure & spandrels of assembly

An ecological network refers to the structure of the interactions between species. In our case, this network is encapsulated in the interaction matrix A , representing all of the

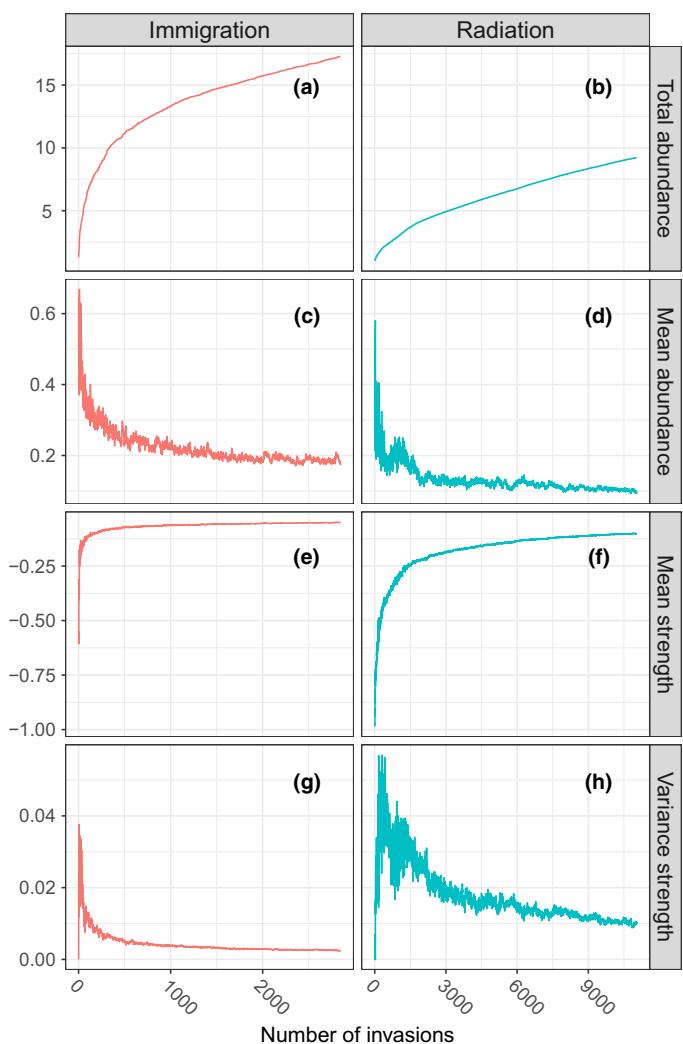


Figure 3 The two invasion scenarios yielded similar overall assembly trends, highlighting the fact that both were subject to the same dynamical selection process. As with species richness, there is a lag in community properties between the immigration (left column, red) and adaptive radiation (right column, blue) scenarios, yet the overall trends between the immigration (left column, red) and adaptive radiation (right column, blue) scenarios are essentially identical. The largest discrepancy is with total abundance, in which the radiation scenario causes species to persist at lower abundances due to intense competition with closely related relatives. Thus, apart from the different patterns in community buildup (Fig. 2), these community-aggregate properties show no clear fingerprint of assembly.

interspecific interactions between species. Thus, to gain precise insight into how assembly affects the structure of the community, we must focus on the ‘structure’ of the interaction matrix. Because each matrix is uniquely determined by its eigenvalues and eigenvectors, a relatively robust way to quantify the structure of a matrix is to focus on the distribution of its eigenvalues, or its ‘spectrum’. If this spectrum deviates significantly from that of a random matrix, then this is a strong indication that the interactions have a non-random structure. Moreover, the spectrum of the interaction matrix is an important aspect of community assembly because it determines whether a feasible community is stable or unstable (May 1973; Goh 1977); if the eigenvalues are strictly negative, then

the community will return to its equilibrium if exposed to sufficiently small perturbations.

In order to determine if a spectrum exhibits a non-random structure, we first need to have an expectation of what a ‘random’ spectrum should look like. Identifying such null models is an ongoing challenge in ecology (Weiher & Keddy 1995; Bello 2012). Fortunately, from a network perspective, the theory of random matrices has solved this problem: if the entries of A are sampled independently from a distribution with known mean and variance, then the spectrum of A will follow the semicircle law (Wigner 1958; Allesina & Tang 2015). Thus, we can calculate the mean and variance of the resulting interaction matrix, and compare the observed spectrum to what would be expected if the network was completely unstructured (see Supplemental Methods). A significant deviation between the semicircle law and the observed spectrum is a strong indication that the network has a non-random structure.

When we calculate the observed spectra, the two different assembly scenarios show pronounced differences in the structure of the interaction matrix (Fig. 4a). In the immigration scenario, the spectrum is essentially indistinguishable from random, as indicated by the fact that the observed histogram (red) closely approximates the random-matrix expectation (black density line and single outlier to the far left). Thus, despite the prominent assembly trends in Fig. 2, the resulting communities are approximately equivalent to what we would obtain if we simply randomly shuffled the interaction coefficients in the matrix. That is, apart from altering the mean and variance of interaction strength, assembly via immigration imparts no clear fingerprint on the network.

In stark contrast, the spectrum of the radiation scenario shows a complex and rich network structure, with a long tail of negative eigenvalues representing clusters of strongly interacting species (Fig. 4b, blue histogram). More importantly, not only is the spectrum highly divergent from random, but it also appears to show strong evidence of ‘selection for stability’. That is, if we were to randomly shuffle the matrix coefficients to obtain an unstructured random network, we would often obtain communities with positive eigenvalues, as indicated by the null distribution overlapping zero. Conversely, if we followed the same matrix randomisation procedure in the immigration case, we would always find stable communities with negative eigenvalues, as indicated by the null distribution being strictly negative. The non-random structure of the radiation network thus appears to carry a fingerprint of stability, and yet this pattern has nothing to do with stability—it is a spandrel of the assembly process.

Network properties

The benefit of inspecting the eigenvalue distribution is that it gives us an exact representation of the overall structure of the network, and furthermore, we have exact analytical expectations for the null distribution. Yet rarely, if ever, will we know the precise null distribution for an empirical network (e.g. see Fig. S8). The next question is therefore if these assembly spandrels propagate to other network properties, or if they can only be detected by comparing the eigenvalue distribution to its random equivalent.

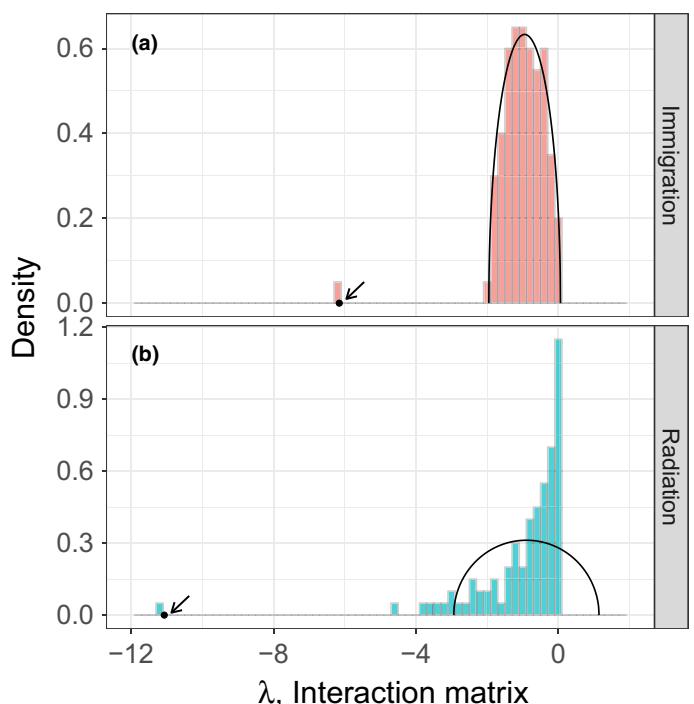


Figure 4 The eigenvalue distribution—or spectrum—of the interaction matrices differed substantially between the two invasion scenarios, showing clear evidence of assembly spandrels. (a) The immigration scenario yielded a network that is indistinguishable from random, with the resulting community perfectly mirroring an unstructured network. The null expectation is given by the black density line and a single outlier (indicated by the arrow), reflecting the mean interaction strength in the network (i.e. Fig. 3e–f). Conversely, (b) the radiation scenario shows a complex and rich network structure, with a long tail of eigenvalues indicating clusters of similar species. Moreover, the radiation network deceptively appears to carry a fingerprint of ‘selection for stability’, due to the fact that the expected distribution significantly overlaps zero.

To address this question, we next explored how these two assembly mechanisms alter the distribution of three network properties: nestedness, modularity and motif counts. These metrics were selected because all are linked to stability and robustness (Bastolla *et al.* 2009; Staniczenko *et al.* 2013; Borelli 2015; Grilli *et al.* 2016; Monteiro & Faria 2016), and because all can be calculated under symmetric competition. This requirement precludes, for example, measures of competitive intransitivity, which, although increasingly linked to biodiversity and coexistence (Soliveres *et al.* 2015; Gallien *et al.* 2017; Maynard *et al.* 2017), assume that competitive outcomes are inherently asymmetric.

The above community-assembly process was repeated 1000 times for each assembly scenario (immigration vs. radiation) until each community reached 100 unique species. The three network properties—nestedness, modularity and motif counts—were subsequently calculated for each of the 1000 networks, following established methods (see Supplemental Methods). However, because these metrics are best defined for binary interactions, we discretised the interaction matrix into ‘strong’ and ‘weak’ interactions. Specifically, for each network, we set the strongest 10% of the interaction coefficients equal to one, and we set the remaining 90% of the a_{ij} equal

to zero. Each discretised network thus contained exactly 495 links (i.e. the top 10% of the $\binom{100}{2} = 4950$ unique interactions) reflecting those species with the strongest competitive effects in the community (Fig. 5). The choice of defining strong vs. weak interactions based on the upper 90th percentile is somewhat subjective; however, using too low a percentile and the networks would be indistinguishable since nearly every species would be connected (since all $a_{ij} \neq 0$); whereas using too high a percentile, and the underlying network structure would be completely destroyed, with only the few strongest links remaining (see Fig. S1).

After converting the interaction matrices to binary matrices, we can plot the distribution of network properties across all 1000 communities (Fig. 6, red and blue histograms). Unfortunately we can no longer borrow from random matrix theory to approximate the null distributions of these properties. Thus, to obtain null expectations we randomly shuffled the entries of each discretised matrix in order to destroy any implicit network structure. This randomisation was conducted so as to ensure that the resulting random networks had the same number of connections and the same degree distribution as the original network (see Supplemental Methods). We then calculated nestedness, modularity, and motif counts for each of these 1000 randomised interaction matrices to obtain the null distribution of values (Fig. 6, gray histograms).

When we look at the resulting distribution of observed vs. randomised network properties (Figs. 6) we once again see clear evidence of assembly spandrels in the radiation scenario relative to the immigration scenario. In the immigration networks, the distribution of nestedness, motif counts and modularity across the 1000 communities is largely indistinguishable from what we observe in the random, unstructured communities. Conversely, in the radiation scenario, the observed distribution of network properties shows significant differences from the corresponding randomised distribution. In particular, the observed radiation networks had higher nestedness, fewer three-chain motifs and higher modularity—all of which

can be interpreted as ‘selection for stability’ (Bastolla *et al.* 2009; Staniczenko *et al.* 2013; Borrelli 2015; Grilli *et al.* 2016; Monteiro & Faria 2016).

Without knowledge of the different assembly mechanisms, we would be justified, based on current theory, in assuming that two different selective forces are at play, with the radiation scenario once again showing evidence of selection for stability. Yet this conclusion would be incorrect—these differences in network properties arise purely because of the way new species join the community.

Incorporating niche overlap

A limitation of the phenomenological Lotka–Volterra model (eqn 1) is that there is no upper bound to the number of species that could coexist—a fact that does not adequately reflect natural systems. Most problematically, without any underlying model governing how species compete, there is nothing preventing species from avoiding competition altogether by sequentially reducing their interaction coefficients (i.e. by finding an empty niche), causing the mean interaction strength to decrease as the community grows (Fig. 2e–f). Thus, an obvious next question is whether these spandrels emerge under increasing levels of realism.

To explore this question, we use a model of niche overlap (Bastolla *et al.* 2005) in which the magnitude of the interaction coefficients is calculated as the relative proportion of shared resources or overlapping traits (eqn S1). Specifically, each species is assigned a k -dimensional resource (or trait) vector. The interaction matrix (and the a_{ij}) is then obtained by calculating the trait covariance among all pairs of species, and rescaling this matrix to within $[-1, 0]$. This approach thus mirrors the concept of the fundamental niche by assuming that each species occupies a point in k -dimensional resource space, and that the intensity of competition is strongest between species with similar niches (Hutchinson 1957; MacArthur & Levins 1967).

We investigate two models of niche overlap. First, we assume there are k binary resources and that each species uses

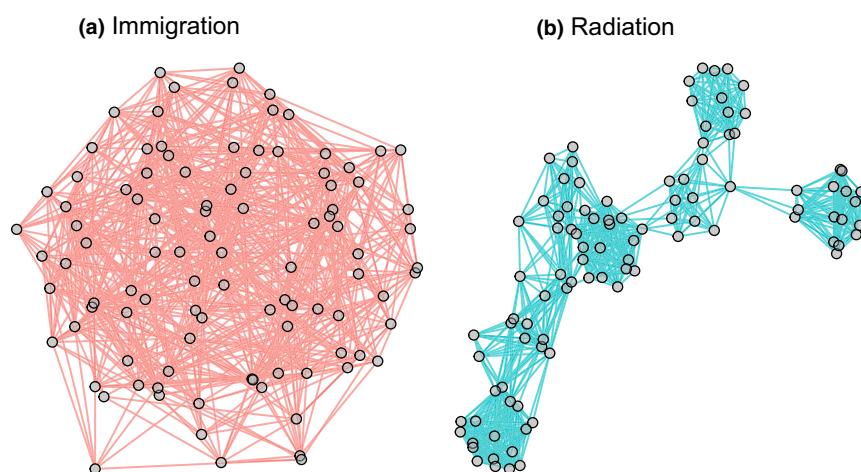


Figure 5 (a) The immigration scenario is indistinguishable from a random network, whereas (b) the radiation scenario leads to clusters of closely related species. Despite the large differences in structure, both communities are dynamically stable, with all species coexisting at equilibrium. The gray vertices denote the 100 species in each community, and the edges denote the strongest 10% (495 of the 4950) of the interspecific interactions in the community.

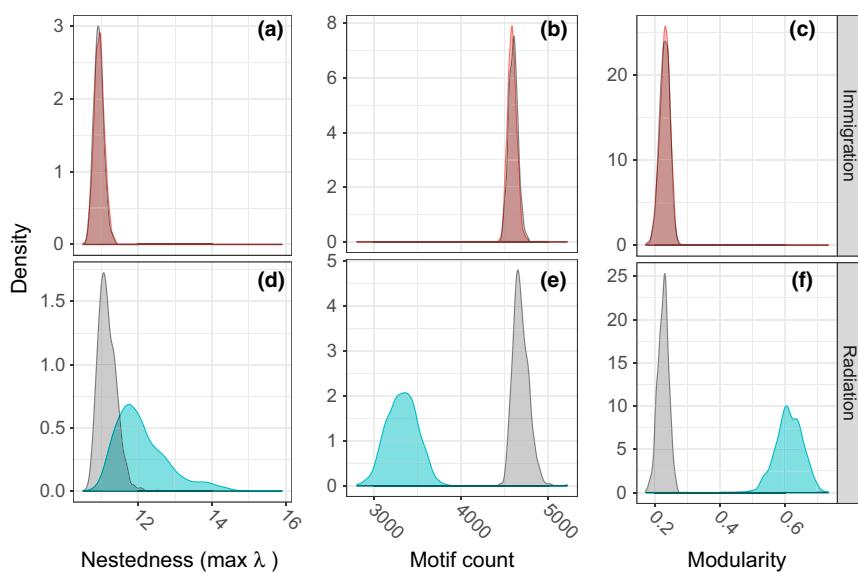


Figure 6 Assembly spandrels emerge regardless of how the network is quantified. Shown are the random distributions (gray histograms) and observed distributions (red and blue histograms) of nestedness, motif counts (total number of three-chain motifs), and modularity across 1000 communities. (a–c) In the immigration scenario, the distribution of network metrics are indistinguishable from random, with the two histograms perfectly overlapping. (d–f) The radiation scenario once again deceptively shows evidence of ‘selection for stability’, as the observed networks have significantly higher nestedness, fewer three-chain motifs and higher modularity (Kolmogorov–Smirnov test of equality: $P < 1 \times 10^{-10}$ for each metric).

a fixed proportion of these resources. Second, we assume there are k continuous resources and that each species’ trait vector denotes their preference for or against each resource. Without loss of generality, we set the number of traits at $k = 200$ for all simulations (Fig. S2). In the continuous traits case, these 200 trait values are originally sampled from a normal $\mathcal{N}(0, 1)$ distribution. In the binary traits case, we assume that each species uses exactly 50% of these 200 resources.

In both trait models, the process for finding new invaders is analogous to the approach taken in the no-trait case (i.e. Fig. 1). The key difference is that we now directly resample or perturb the invader’s trait values rather than their interaction coefficients. In the binary case, we randomly populate a vector with 100 ones and 100 zeros (under immigration), or we randomly select a parent’s binary trait vector (under radiation). We then ‘flip’ a fixed proportion of these binary traits to their opposite, done in such a way so as to ensure that each species continues to use exactly 50% of the resources (see Supplemental Methods). In the continuous case, we either resample entries from a normal $\mathcal{N}(0, 1)$ distribution (under immigration), or we perturb the parent’s values by adding a random vector with entries sampled from a $\mathcal{N}(0, 0.03)$ distribution (under radiation). Once we obtain the new trait vector, we recalculate the trait covariance between species i and j to obtain the a_{ij} coefficients, and we check the invasion criterion in eqn 2. This process is repeated until a successful invader is found, and iterated until each community reaches 100 species.

Niche overlap and spandrels of assembly

As with the unstructured Lotka–Volterra model, the trait-based radiation scenarios required substantially more invasions to reach comparable community sizes to the

immigration scenarios (Fig. S3). Yet, apart from this, the overall trends are once again nearly identical between the two scenarios (Figs. S4–S5). The notable distinction is that the mean interaction strength now converges to -0.5 , rather than 0.0 as in the unstructured model (Figs. S4–S5 vs. Fig. 3). This result highlights the inherent symmetry of the niche space: species cannot avoid interacting, and so new invaders tend to be more successful if they occupy a portion of the niche space that is the least crowded. This process in turn leads to the species being approximately uniformly distributed across the k -dimensional trait space.

The next question is how these two assembly constraints affect the structure of the network, as measured by the spectrum of the interaction matrix. In the resource-overlap models, the null expectation for this spectrum is no longer given by the semicircle law due to the inherent correlation structure embedded within the matrix. That is, if species i has a strong interaction with species j and k , then species j and k must also have a relatively strong interaction with each other, as all three species must occupy a similar region of trait space.

Fortunately, once again, a key result in random matrix theory applies to this exact setting: given a rectangular matrix with random entries, then the corresponding covariance matrix follows the Marchenko–Pastur distribution (Marchenko & Pastur 1967). In the resource-overlap models, the interaction matrices are calculated as the scaled covariance between species’ trait vectors (eqns S2 & S3). Thus, the null expectation is that the spectrum of the interaction matrices should, in the absence of any network structure, approximate a Marchenko–Pastur distribution (see Supplemental Methods).

After plotting the resulting eigenvalue distributions (Fig. 7), we see that the null expectations in niche-overlap models

(black density lines) differ substantially from those in the no-trait scenarios. This is because the Marchenko–Pastur law for rectangular matrices results in a distribution that is peaked and highly skewed, rather than symmetric and semicircular. However, apart from this distinction, the overall effect of assembly is nearly identical between the niche-overlap models and the basic Lotka–Volterra model: the immigration scenario perfectly maps onto the Marchenko–Pastur distribution, while the radiation scenario exhibits a complex network structure that deviates from random expectation.

As with the unstructured model, these spandrels in the radiation scenarios simply reflect clusters of closely related species with similar trait preferences. One key distinction, however, is that in both scenarios the eigenvalues are necessarily non-positive due to the fact that the interaction matrix is the negative of the scaled covariance matrix (eqns. S2–S3), and is therefore negative definite (see Supplemental Methods). Accordingly, we no longer see differing levels of ‘selection for stability’ between the immigration and radiation cases, as both null distributions are strictly negative and do not overlap zero (black density lines in Fig. 7). However, if we did not know the appropriate null distribution and we proceeded to (incorrectly) estimate the null distribution by randomly shuffling the interaction matrix or by applying the semicircle law, then we would obtain a null distribution that significantly overlaps zero. Thus, we would arrive at the incorrect inference that *both* of these networks show selection for stability (i.e. mirroring the inference in Fig. 4b). Yet this stability is simply due to the fact that species’ interactions are dictated by their

shared covariance in trait space, and it otherwise has nothing to do with the selective forces at work.

Lastly, when we calculate modularity, nestedness and motif counts for the niche-overlap models, we see a clear fingerprint of assembly imparted on the networks, with the resulting patterns closely mirroring the unstructured setting (Figs. S7–S6). Once again, the radiation networks deceptively exhibit a strong signal of ‘selection for stability’, and the immigration networks closely match a random, unstructured network. Taken collectively, these results highlight that ecological spandrels can be robust to different underlying model assumptions.

DISCUSSION

The distinction between selective and non-selective forces dates back to the foundations of modern ecology. In *Origin of the Species*, Darwin noted that, ‘natural selection has been the most important, but not the exclusive, means of modification’ (Darwin 1859). That is, biological systems are not only a result of selective forces but also of the mechanisms that determine how and why new variation is introduced. Ecological networks are no exception—they arise due to the interplay between assembly forces and selective forces (Nee 1990). Our work demonstrates that different assembly processes leave different fingerprints on the network, such that it would appear that different selective forces are at work. This inference, however, would be incorrect; these non-random patterns are spandrels of ecological assembly.

Although ecological spandrels are largely uninformative of stabilising forces operating in the system, they can still have important ecological implications. A key feature of a spandrel is that it reflects the historical processes shaping the system (Solé & Valverde 2006). From a network assembly perspective, obtaining such knowledge is particularly difficult given that the formation of ecological networks can involve processes that occur over evolutionary timescales (Juan *et al.* 2000; Kashtan & Alon 2005; Guimarães *et al.* 2011). Thus, by reflecting the underlying assembly rules, network spandrels have the potential to provide key insight into the historical processes shaping empirical networks.

The fact that assembly history affects the structure of biological networks is not altogether surprising. The radiation scenario used here is similar to previous models of duplication-rewiring in evolutionary networks (Enemark & Sneppen 2007; Solé & Valverde 2008), and Valverde *et al.* (2017) recently demonstrated that similar models can lead to emergence of nestedness in mutualistic networks. Indeed, various ecological and evolutionary processes have been linked to network structure, including the optimisation of total community abundance (Suweis *et al.* 2013) and co-evolution of species (Nuismer *et al.* 2013; Ponisio & M’Gonigle 2017). A challenge in such work, however, is determining whether these emergent patterns arise because of how new features are added to the system, or if instead they arise because of the selective mechanisms that subsequently determine which features persist (Gould & Lewontin 1979; Barrett & Hoekstra 2011). Those few studies that have explored the impacts of different assembly rules on community

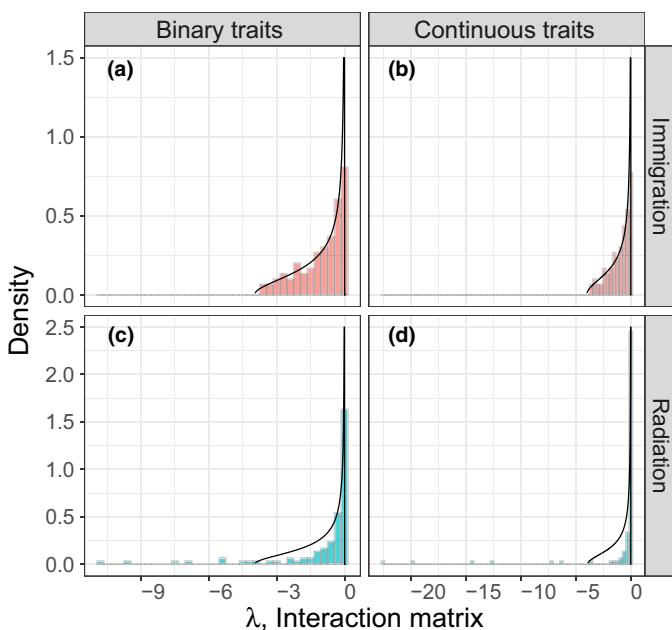


Figure 7 When species’ interactions are dictated by the degree of niche overlap, the shape of the null distribution changes, but the effect of assembly remains the same. (a,b) Regardless of whether resources are binary or continuous, the observed spectrum in the immigration scenario once again maps onto the null distribution of an unstructured network, now given by the Marchenko–Pastur distribution (black density lines). (c,d) Conversely, the spectra of the radiation scenarios show complex network structures that deviate significantly from random.

organisation (e.g. Powell & McKane 2009) often focus on ‘mean-field’ aggregate quantities such as species richness or mean abundance (i.e. Fig. 3) rather than network structure. Here, by using two different processes for generating new species, we clearly show that these network spandrels are directly attributable to different assembly rules and not different selective forces.

A prevalent concept in ecology is that non-random patterns indicate deviations from the ‘null’ case (Weiher & Keddy 1995; Bello 2012; Veech 2014). Yet, as these results illustrate, this assumption can be problematic. The two assembly scenarios were subject to identical selective forces, and yet one community showed deviations from random expectations and the other did not. Rarely do null-model approaches address the fact that different assembly constraints may alter the structure of the community in non-random ways, nor do they address the fact that some important ecological processes (e.g. immigration) may lead to patterns that mirror random expectations. The fact that assembly constraints can promote non-random patterns in no way negates the importance of null models in ecology, but it does highlight the need to better understand the role of assembly in order to make correct inference about the implications of departures from randomness.

A clear extension of this work is exploring how assembly spandrels affect other aspects of community structure. One interesting feature of the radiation scenario is that we can keep track of the phylogeny of the community: each species is connected to its progenitor (extant or extinct), and one could therefore test how different assembly scenarios shape the phylogenetic tree (or functional trait diversity) of extant species. Knowledge of how assembly history constrains the phylogenetic tree can have large implications for inferring underlying assembly mechanisms from empirical patterns (Mayfield & Levine 2010). Important next steps are thus to explore how more complex colonisation constraints affect the phylogenetic and functional structure of communities (e.g. the arrival of niche specialists vs. niche generalists; Fukami *et al.* 2007), via the incorporation of realistic models of phylogenetic diversification and trait evolution (Kashtan & Alon 2005; Guimarães *et al.* 2011; Mouquet *et al.* 2012; Nuismer *et al.* 2013).

Each unique ecological and evolutionary process—such as asymmetric vs. symmetric competition, predator–prey dynamics, facilitation, co-evolution, etc.—will likely give rise to a unique set of assembly spandrels. Indeed, there are certain to be some ecological processes that are relatively immune to assembly history (Capitán *et al.* 2009; Fukami & Nakajima 2011). Our goal is thus not to say when and where spandrels will arise in realistic natural systems, but rather to provide a simple example of how assembly rules cannot be discounted *a priori* when interpreting network structure. Moreover, it is important to note that even subtle differences in assembly rules can alter the shape of the network. For example, if we repeat the immigration scenario by instead sampling new species uniformly from the space of feasible invaders (rather than by resampling coefficients one at a time), we obtain a slightly different spectrum (Fig. S8). From an ecological perspective, these different assembly rules are akin to making different assumptions about the processes that give rise to new biological variation (Morton & Law 1997; Law 1999). The appropriateness of any particular

rule—and the presence or absence of corresponding spandrels—will thus depend on the specific ecological system of interest.

The assembly models we investigate here are simple representations of natural processes. Yet this simplicity does not negate the overarching problem: we have no clear expectation for how different community assembly processes should shape ecological networks. On one hand, the inclusion of more complex and realistic dynamics—such as environmental variability or spatially-structured interactions—may lead to fewer network spandrels by, in effect, ‘averaging out’ assembly history or by allowing more diverse species to persist than would otherwise be possible in a well-mixed system (Molofsky *et al.* 2001; Schreiber & Killingback 2013; Tucker & Fukami 2014; Maynard *et al.* 2017). On the other hand, more complex systems may provide more opportunities for the emergence of unique and unpredictable patterns (Kashtan & Alon 2005; Reichenbach *et al.* 2007), which impart their own fingerprints on the network. The fact that we have no clear expectation for how ecological complexity should affect network spandrels highlights important grounds for future research.

By demonstrating that a failure to account for historical assembly can lead to incorrect inferences about stability, we highlight a largely overlooked area of ecological research. In evolutionary biology and cellular genetics, the widespread realisation that assembly constraints and selective processes can lead to identical biological patterns has led to more rigorous methods for isolating the links between organismal function and adaptive selection (Solé & Valverde 2006; Forber 2009; Barrett & Hoekstra 2011). Analogously, an appreciation of ecological network spandrels will hopefully spur the development of more rigorous methods for disentangling assembly forces from selective forces (Nee 1990). Such knowledge is necessary if we are to make robust inference about the underlying mechanisms that shape empirical networks. Obtaining a more comprehensive understanding of the importance and pervasiveness of these assembly artefacts will require the integration of various aspects of community assembly theory and network stability analysis. By doing so, we have the potential to gain insight into the historical processes structuring natural communities, and better understand the patterns and processes shaping ecological networks.

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AUTHORSHIP

SA conceived of the idea. DSM and CAS conducted the analyses. DSM wrote the manuscript with input from CAS and SA. All authors assisted with revisions.

DATA ACCESSIBILITY STATEMENT

The code needed to reproduce all results presented in this article can be downloaded from https://github.com/dsmaynard/network_spandrels.

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