Notes

Biodiversity maintenance may be lower under partial niche differentiation than under neutrality

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Abstract. Niche differentiation is normally regarded as a key promoter of species coexistence in competitive systems. One might therefore expect that relative to neutral assemblages, niche-differentiated communities should support more species with longer persistence and lower probability of extinction. Here we compare stochastic niche and neutral dynamics in simulated assemblages, and find that when local dynamics combine with immigration from a regional pool, the effect of niches can be more complex. Trait variation that lessens competition between species will not necessarily give all immigrating species their own niche to occupy. Such partial niche differentiation protects certain species from local extinction, but precipitates exclusion of others. Differences in regional abundances and intrinsic growth rates have similar impacts on persistence times as niche differentiation, and therefore blur the distinction between niche and neutral dynamical patterns—although niche dynamics will influence which species persist longer. Ultimately, unless the number of niches available to species is sufficiently high, niches may actually heighten extinction rates and lower species richness and local persistence times. Our results help make sense of recent observations of community dynamics, and point to the dynamical observations needed to discern the influence of niche differentiation.

Key words: community assembly; community dynamics; competitive coexistence; immigration; local persistence time; neutral dynamics; Partial niche differentiation; stochastic niche dynamics.

INTRODUCTION

Niche differentiation is widely considered a prime force behind species coexistence, and thus instrumental in maintaining biodiversity. Niche differentiation stabilizes communities by guaranteeing positive growth rates of rare species (Chesson 1991, 2000). Without such stabilization, coexistence is only temporary, and biodiversity can only be maintained if gains from immigration or speciation compensate losses to competitive exclusion or drift as posited in neutral theory (Hubbell 2001).

Views on the implications of niche differentiation for biodiversity maintenance mostly come from deterministic community models with no immigration. However, stochastic formulations, which model the influence of variability in finite populations whose deterministic details are unknown or unrelated to species differences, are more relevant for natural systems. In such settings, coexistence is defined in a probabilistic sense (Schreiber 2015).

Furthermore, many if not most communities in nature are subject to propagule pressure from regional pools. In such open-community scenarios, species may persist for a substantial period of time due to mass effects, and extinction is not an absorbing state since later re-colonization is always possible. One measure of diversity maintenance in this context is species mean persistence time – the average time between introduction through immigration and extirpation through drift or competitive exclusion.

Persistence times have been studied as indicators of ecological processes (Leigh et al. 1993, Magurran and Henderson 2003), and have been explored theoretically in the context of neutral dynamics (Leigh et al. 1993, McGill et al. 2005, Nee 2005, Pigolotti et al. 2005, Bertuzzo et al. 2011, Condit et al. 2012, Segura et al. 2017). Recent studies found that stabilizing niche differentiation considerably prolongs persistence times (Pigolotti and Cencini 2013, Carroll and Nisbet 2015). However, the niche scenarios proposed in these studies tend to be extreme. For example, Pigolotti and Cencini (2013) used a stochastic version of a simplified Lotka-Volterra model where all species interactions are identical except that competition is stronger within than across species (Haegeman and Loreau 2011). This corresponds to a biological scenario where all species

stably coexist and in this sense occupy their own niche. The authors found that niche stabilization increased species persistence times compared with neutral assemblages. Given this extreme degree of stabilization, the higher persistence is not surprising.

A niche for every species is unlikely in highly diverse systems such as tropical forests, where it has been argued that the niches-to-species ratio can be low (Hunter and Foster 1986, Holt 2006). Even in lower diversity systems, there is no clear evidence that all species can mutually invade from low abundance. Empirical demonstration of frequency dependence is rare (Siepielski and McPeek 2010, but see Adler et al. 2010, Chu and Adler 2015). On the other hand, there is evidence suggesting competition increases with higher phenotypic similarity (Johansson and Keddy 1991, Jiang et al. 2010, Burns and Strauss 2011). Models with this type of competitive structure predict limits to similarity between species that can coexist in stable equilibrium; those outside these limits are eventually excluded by stronger competitors (MacArthur and Levins 1967). However, some species are excluded faster than others, resulting in the spontaneous formation of transient clusters of similar species (Scheffer and van Nes 2006, Fort et al. 2009). In particular, those with the most unfavorable traits might be excluded faster than under pure drift. Given a continuous supply of immigrants, a neutral scenario may even sustain more species.

In addition to niche relations, other types of species differences also affect local dynamics. Environmental filters may cause non-stabilizing fixed differences in species growth and death rates, which can dramatically change richness, persistence times, and abundance distributions relative to neutrality (Zhou and Zhang 2008, He et al. 2012). Furthermore, immigration will promote local persistence of regionally common species over regionally rare ones. Although immigration can stabilize communities as it pushes local relative abundances towards regional relative abundances, it is conceptually different from stabilization caused by ecological advantages to rare species, i.e., niches. One wonders whether the effects of niche differences on persistence are similar or fundamentally different from those of species differences unrelated to niches.

Here we hypothesize that a local species assemblage where the number of niches available is less than the number of species in the regional pool may have lower diversity and shorter persistence times on average than a completely neutral community of the same size and subject to the same propagule pressure. To test that hypothesis, we perform a simulation-based study of an open local community under stochastic niche dynamics with a adjustable number of niches. We compare species richness, persistence times, and extinction rates against a fully neutral assemblage. We then see how results change when we add differences in regional abundances, immigration, and intrinsic growth rates. Finally, we test how the number of niches affects comparison with neutrality.

METHODS

Simulated dynamics

We use a lottery model to implement stochastic dynamics in a local community subject to immigration from a regional pool. The local community has a fixed number of individuals, and in each time step a single individual dies and is replaced by a new individual. When a death occurs, the probability that it befalls species i is $\sum_j A_{ij}N_iN_j / \sum_{kl}A_{kl}N_kN_l$, where N_i is species i's abundance and the coefficient $A_{ij} > 0$ reflects the degree of competition between species i and j. The new recruit can be either a local offspring with probability $1 - m$ or an immigrant from the regional pool with probability m. If it is a local offspring, the probability that species i is chosen at this stage is $r_iN_i / \sum_j r_jN_j$, where r_i is the intrinsic growth rate of species i. If the recruit is an immigrant, species i is chosen with probability given by its relative abundance in the regional pool p_i, where $\sum_i p_i = 1$.

If we set all r_i = constant and $A_{ij} = 1$, then per capita birth and death probabilities are the same across species and this model becomes identical to Stephen Hubbell's (2001) neutral community model. Our model is an extension of Hubbell's model where we allow for species differences, which appear as differences in the r_i and A_{ij}. The niche mechanism consists of the map between species traits and the competition coefficients A_{ij}. We note that we are placing density-dependent competitive effects on deaths, but preliminary tests revealed that none of our results change qualitatively by placing them on births instead. We also note that our model is similar to classical Lotka-Volterra dynamics, though in stochastic form. In fact, we numerically verified that it yields the same qualitative behavior as a Gillespie implementation of stochastic Lotka-Volterra dynamics (see Appendix S1).

By fixing community size, we can focus on the impact of competition; otherwise, fluctuations in community size would also affect dynamics regardless of the competitive structure. To facilitate comparison we use the same community size in all our scenarios. We set the local community size at 21,000 individuals, which mirrors a typical real-world scenario of trees exceeding 10 cm diameter at breast height in a 50-ha plot of tropical forest (e.g., Barro Colorado Island, Pasoh Forest Dynamics Plot). We also verified that using a different community size had no qualitative impact on our results. Abundances in the regional pool, which contains 150,000 individuals and 400 species, are either identical or follow a neutral logarithmic (log-series) distribution (Volkov et al. 2003). Additional simulations verified that a larger regional pool had no impact on quantitative results.

We start the local community with a random draw of offspring from the regional pool, and then simulate dynamics for 50 million death and replacement events, at which point species abundance distributions appear

stationary. We then run for another 50 million death and replacement events while keeping track of all introduction and extirpation events, for a total of 100 million steps, corresponding to roughly 5,000 community turnovers. At the end of a run, we measure species richness, mean extinction rate, and species persistence times. We calculate the latter as the average number of steps that each species remained in the local community between being introduced through immigration and being extirpated due to competitive exclusion or drift. Given the low variation in these indices across replicates of the same scenario (see *Results*), we decided that 10 replicates of each is sufficient.

Note that although we are measuring time in terms of events (death immediately followed by replacement), we are not necessarily assuming constant intervals. If time is measured in terms of days or years etc., there will be an exponential distribution of intervals between consecutive events (assuming deaths follow a Poisson process). Approximating the rate of deaths per unit time as fixed, the expected value of the relative persistence times measured in physical time units will be very close to the relative persistence times measured in events.

All simulations were coded in the R computer language (version 3.4.1, with code available on GitHub (D'Andrea 2017; version R Core Team 2017).

Scenarios

We pin competition to phenotypic (trait) similarity by setting $A_{ij} = \exp\left[-\left(\frac{x_i - x_j}{w}\right)^4\right]$, where $x_i = (i - 1)/400$ is the trait value of species i (traits range between 0 and 1). This is a commonly used decreasing function of trait difference (Hernández-García et al. 2009, Pigolotti et al.

2010). Another common choice is Gaussian competition, where the power 4 in the exponential function is replaced with 2, but that has been shown to be mathematically idiosyncratic (Hernández-García et al. 2009), and leads to very slow competitive sorting. The scale constant w determines how quickly competition decreases with trait difference. When $w \approx 0$, each species competes only with itself, corresponding to a case where each species has its own niche (complete niche differentiation). In the opposite extreme $w \to \infty$, all species compete equally in the same single niche (neutral competition). In between is partial niche differentiation, where there are fewer niches than species: competition is stronger between more similar species, and only those sufficiently niche-differentiated would be able to coexist in the absence of immigration.

By analogy with common statistical terminology for null and alternative hypotheses, we will refer to communities lacking niche stabilization as H_0 assemblages, and those with niche stabilization as H_1 assemblages. In terms of our parameters, H_0 assemblages have $w \to \infty$ and hence $A_{ij} = 1$ between all species pairs (neutral competition), whereas in our H_1 assemblages w is finite and A_{ij} vary based on trait differences.

Table 1 describes all our scenarios and our corresponding hypotheses as to the impact caused by the factor being varied. Our first scenario, termed the Baseline, isolates the impact of partial niche differentiation by considering H_0 and H_1 assemblages where all species have identical regional abundances and intrinsic growth rates, so that the only differences between species are niche differences. Next we check how niche differences affect persistence when acting in concert with other species differences that do not contribute to stable coexistence. In Variants 1 and 2, some species immigrate more

TABLE 1. Variants 1 through 4 are identical to the baseline scenario except where indicated in the Description and Parameters columns. Settings are applied to both the neutral (H_0) and niche (H_1) simulations where applicable.

Scenario	Description	Parameters	Hypothesis
Baseline	Isolate differences between neutral competition (H_0) and partial niche differentiation (H_1)	$p_i = const.$ $r_i = const.$ $m = 0.01$ $w = 0.063$	Some species in H_1 will have enhanced persistence and others lessened persistence relative to H_0
Variant 1	Some species are more abundant than others in regional pool → Inhomogeneous immigration	$p_i \sim \log\text{-}series$	Even in H_0, some species will be more prone to extinction than others due to lower rescue effect. Outcomes of H_0 and H_1 will be more similar than in Baseline
Variant 2	Same as Variant 1 but species have higher dispersal ability → Higher immigration	$p_i \sim \log\text{-}series$ $m = 0.1$	Higher immigration increases persistence times and magnifies the effects of regional abundances relative to internal dynamics. Outcomes of H_0 and H_1 even more similar than in Variant 1
Variant 3	Metabolic costs or other physiological limitations cause lower intrinsic growth of species with extreme trait values	$r_i = x_i(1 - x_i)$	Species with higher intrinsic growth will have higher persistence and lower extinction rates. Effect is stronger on H_0 assemblage, bringing H_0 outcomes closer to H_1 than in Baseline
Variant 4	Intrinsic growth rates are determined by factors unrelated to the niche trait, such as environmental filtering for unrelated traits	$r_i \sim U(0, 1)$	Qualitatively similar impact as Variant 3

frequently than others because of differences in regional abundances. In Variants 3 and 4, some species have higher intrinsic growth rates than others because of physiological constraints or environmental filters. In Variant 2, we additionally test for the impact of immigration by giving all species ten times the dispersal ability used in the rest of the study ($m = 0.1$ vs. $m = 0.01$. As a reference point, immigration rates at Barro Colorado Island are estimated at $m = 0.08$, Chisholm and Lichstein 2009).

Finally, we look at the impact of varying the number of niches available to our 400 species. We define the number of niches as the number of species that can coexist without immigration in the deterministic formulation of our model. In all scenarios shown in Figs. 1 and 2 we set $w = 0.063$, which leads to 12 niches and thus about 33 species per niche. By lowering parameter w we raise the number of niches from 12 to 400 (1 species per niche, i.e., full niche differentiation). For this part, we use Variants 1 and 2, where regional abundances are logarithmically distributed as in a neutral metacommunity (Volkov et al.

2003). Results for Variant 1 (where $m = 0.01$) are shown in Fig. 3, and results for Variant 2 (where $m = 0.1$) are shown in the supporting information.

RESULTS

When regional abundances and intrinsic growth are identical across all species (Baseline scenario), the assemblage with partial niche differentiation (H_1) stands in high contrast with the neutral assemblage (H_0), as shown in Fig. 1. In H_0, persistence times show no relation to species trait values (Fig. 1A) and do not correlate with species abundances observed at the end of the simulation (correlation index $\rho_{\log(N),\log(T)} = 0.008$). By contrast, in H_1 persistence times and species abundances are highly non-random (Fig. 1B), and correlate strongly with each other ($\rho_{\log(N),\log(T)} = 0.86$, see also Appendix S2: Fig. S1).

A distinctive pattern is seen along the trait axis: species lump together, and the lumps or clusters are separated by
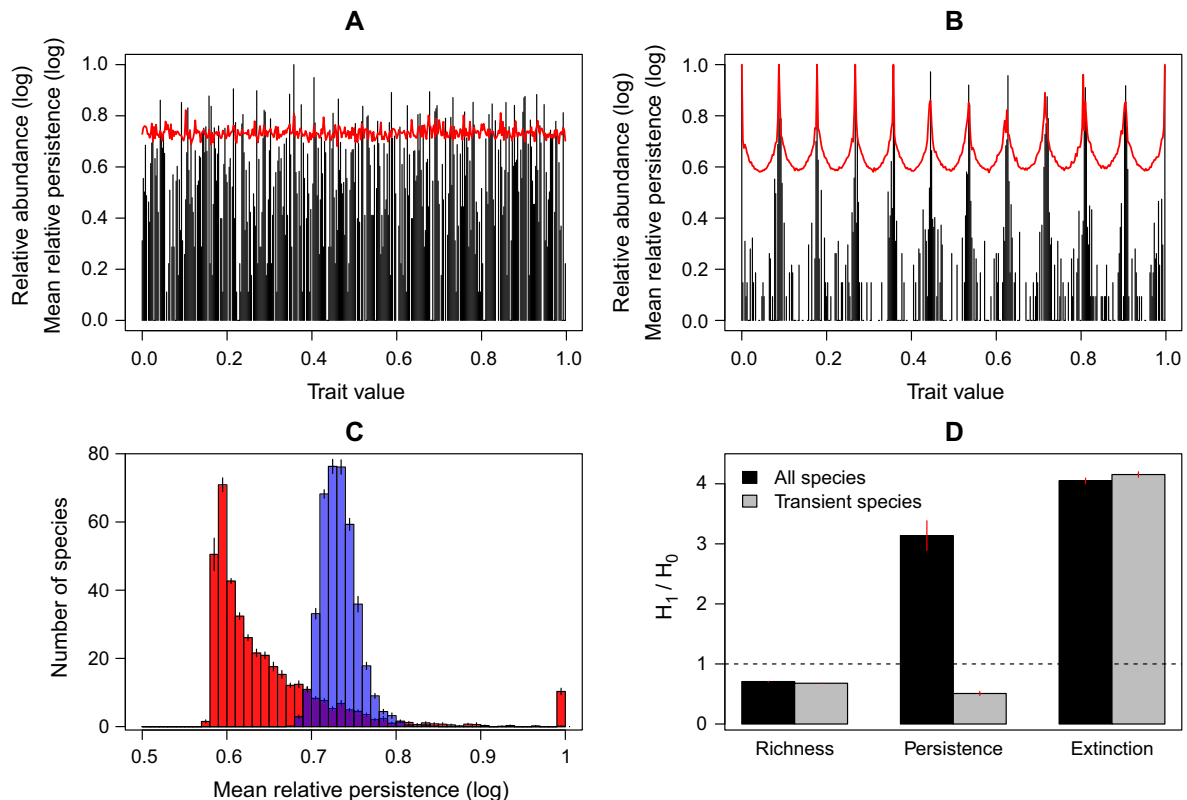

FIG. 1. (A, B) Species abundances and persistence times plotted against relative trait values in an example H_0 assemblage (A) and H_1 assemblage (B). Stems show log N/log N_{max}, where N are species abundances and N_{max} is the highest abundance observed. Red lines show log T/ log T_{max}, where T are species mean persistence times and $T_{max} \simeq 24{,}000$ community turnovers is the maximum possible persistence time, corresponding to our entire tracking period (1 community turnover = 21,000 simulation steps). (C) Number of species by mean persistence time, log T/log T_{max}, in the baseline assemblages with no stabilization (H_0, blue bars) and partial stabilization (H_1, red bars). Shown are averages across ten replicates. Error bars show standard error of the mean. (D) Comparison of species richness, community-averaged persistence time, and community-averaged extinction rates between baseline H_1 and H_0 assemblages. Bars show average ratio H_1/H_0 across ten replicates, error bars show standard error of the mean. [Color figure can be viewed at wileyonlinelibrary.com]
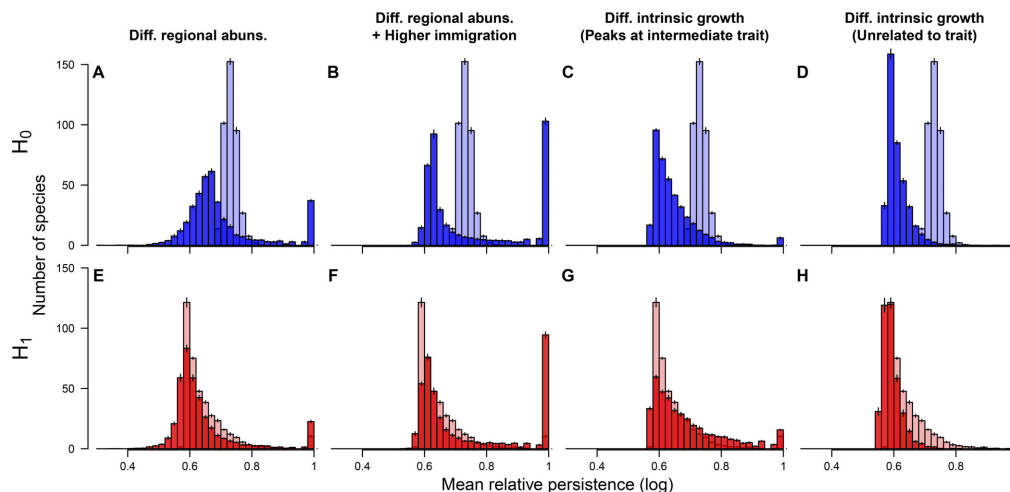
FIG. 2. Comparison of persistence time distribution, log T/log T_{max}, between baseline (pale colors) and variant scenarios (dark colors) as described in Table 1. Top row shows H_0 assemblages, bottom row shows H_1 assemblages. Results shown are averaged across ten replicates of each scenario, with error bars showing the standard error of the mean. (A, E) species have random, logarithmically distributed regional abundances, independent of trait values; (B, F): logarithmically distributed regional abundances and higher immigration rate ($m = 0.1$); (C, G) intrinsic growth rates r_i peak at the center of the axis and drop to zero at the edges; (D, H) species have random, uniformly distributed r_i values, independent of trait values. [Color figure can be viewed at wileyonlinelibrary.com]

gaps of low abundance (and corresponding low persistence times). This clustered pattern occurs in all our simulations (see Appendix S2: Figs. S4–S6, S8), and indeed has received attention in the recent literature on niche dynamics (Holt 2006, Scheffer and van Nes 2006, Fort et al. 2009, 2010, Pigolotti and Cencini 2013, D'Andrea and Ostling 2016). We verified in our simulations that if immigration is turned off, the clusters eventually disappear, and one species remains per each cluster. Each cluster therefore represents a niche, and under immigration each niche is occupied by more than one species. The residents are the species best adapted to their niche, and are the ones that remain in the absence of immigration.

There is much higher variation in mean persistence time across species in the partially stabilized assemblage than the neutral counterpart (Fig. 1C; also compare red curves in Fig. 1A,B). The histogram of persistence times (Fig. 1C) reveals that (1) a few species in H_1 but none in H_0 are residents, i.e. were present throughout the tracking period of the simulation, never going extinct; (2) the vast majority of species in H_1 not only are transient but in fact have lower persistence times than in H_0. Residents benefit from stabilization and can in principle remain indefinitely (barred stochastic fluctuations), thus heavily driving mean persistence times in H_1. Indeed if residents are discounted, the average persistence time in H_1 drops from higher to lower than the neutral assemblage (Fig. 1D). Importantly, the outsize influence of residents on community-averaged persistence times does not translate to higher diversity or lower extinction. In fact, both species richness and community-averaged extinction rates are lower in the partially stabilized assemblage

than under neutrality, whether or not residents are accounted for (Fig. 1D).

When some species are more abundant than others in the regional pool causing differences in immigration rates (Variant 1), the persistence time distribution shifts towards the extremes (Fig. 2A,E): on one hand, transients have shorter persistence times compared to when the pool is homogeneous; on the other hand, the neutral community now also has residents, and in H_1 the number of residents is higher than before. These new residents arise not from stabilization but because of their comparatively high regional pool abundance (Appendix S2: Fig. S2). As a result, H_0 and H_1 now have more similar distribution of persistence times than in the Baseline scenario (compare Fig. 2A,E).

Keeping the differences in regional abundances and increasing immigration tenfold (Variant 2), we see most persistence times increase and many species become residents in both H_0 and H_1 assemblages (Fig. 2B,F, compare with Fig. 2A,E). A few species now have actually lower persistence times due to regional rarity. Overall, regional abundances become stronger determinants of persistence times compared with the lower immigration scenario. Again, H_0 and H_1 communities are more similar to each other than in the Baseline scenario (compare Fig. 2B,E). It should be noted that although high immigration may make the persistence time distributions essentially indistinguishable, niche differentiation still influences which species are residents (Appendix S2: Fig. S3). We also note that a comparable increase in immigration when the pool is homogeneous trivially makes all species residents in both the H_0 and H_1 assemblages (results not shown).
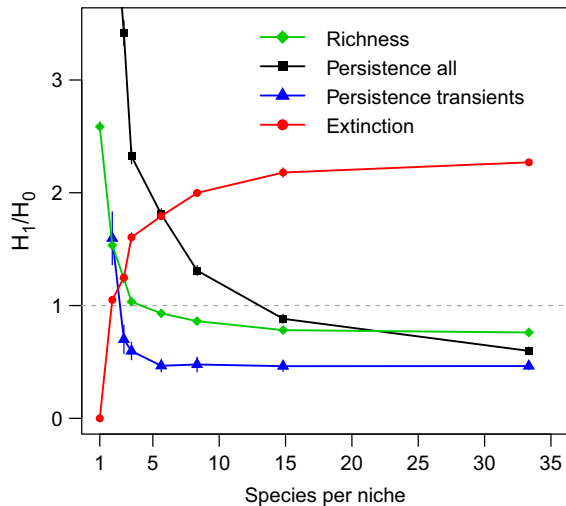
Fig. 3. Comparison of richness, community-averaged persistence times, and community-averaged extinction rates between neutral assemblages (H_0) and partially differentiated assemblages (H_1) with increasing number of niches and fixed regional diversity. Data points show the ratio between the H_1 and H_0 assemblages, error bars show one standard error of the mean, calculated across 10 replicates. Persistence times are shown averaged across all species in the community (black) and across transients (blue). As the number of niches increases from 12 to 400, the number of species per niche decreases from 33 to 1 species per niche. All measured quantities cross the neutral value (dashed gray line) at different points. In the limit of full niche differentiation (one species per niche), extinction is zero and local persistence and richness are maximal. Regional abundances are logarithmically distributed, while all other parameters are set as in the Baseline scenario (Variant 1, see Table 1. Compare similar plot for Variant 2 in Appendix S2: Fig. S7). [Color figure can be viewed at wileyonlinelibrary.com]

The introduction of intrinsic growth advantages to species with intermediate trait values (Variant 3) dramatically lowers persistence times for most species in H_0 compared to the Baseline, while promoting those few species with the highest intrinsic growth to resident status (compare pale- and dark-colored bars in Fig. 2C). The effects on the H_1 assemblage are more subtle, with persistence times actually increasing for several species (Fig. 2G), and correlating negatively with intrinsic growth ($\rho_{r,\log T} = -0.2$, see also Appendix S2: Fig. S4). However, the qualitative shape of the H_1 persistence time distribution is unchanged, indicating that intrinsic growth rates have a small effect on H_1 exclusion dynamics relative to frequency-dependent competition. Again, the H_0 and H_1 persistence time distributions become less distinguishable compared with the baseline where all intrinsic growth rates are identical (compare Fig. 2C,G).

Differences in intrinsic growth rates that are unconnected to the niche-related trait (Variant 4) shorten the persistence times of almost all species in both the H_0 and H_1 assemblages, but once again the effect is much stronger on the assemblage lacking stabilization

(Fig. 2D,H). As with previous variants, niche and neutral communities are more similar than in the Baseline.

In summary, differences in regional abundances and intrinsic growth have a qualitatively similar effect on persistence times as niche differentiation: persistence times of most species is very short, while those of a few species is indefinitely long. As a result, the persistence time distribution is qualitatively similar whether or not niche differentiation is present. On the other hand, relative to the Baseline scenario where all regional abundances and intrinsic growth rates are identical, the effect is much stronger on H_0 communities than H_1 communities (compare the dark- and light-shaded bars in the top and bottom rows of Fig. 2).

As we increase the number of niches while keeping regional diversity fixed, all our biodiversity metrics improve from worse to better than in the neutral community (Fig. 3). In particular, as fewer species compete for the same niche tending towards full niche differentiation (one species to one niche, on the left end of the graph), extinction tends to zero and richness escalates. Persistence times increase dramatically. Most of the improvement stems from the larger number of residents; persistence across transients also improves, but more slowly (compare blue and black curves in Fig. 3, see also Appendix S2: Fig. S5).

We note that the specific degree of stabilization required for higher persistence in the H_1 assemblage depends on the particulars of the community, such as immigration rates and niche axis geometry (Appendix S2: Figs. S6, S7), but the qualitative results are the same: biodiversity maintenance can be actually lower in a community with niches compared with a neutral community, unless the number of niches is sufficiently high.

DISCUSSION

By building on the framework of neutral models (Alonso et al. 2006), our study sheds light on biodiversity maintenance in an open community where species similarity begets competition and the number of species exceeds the number of niches. Partial niche differentiation stabilizes species abundances and may indefinitely prolong local persistence times of certain species, but at the community level it does not guarantee higher richness, longer persistence times, or lower extinction rates. Differences in regional abundances and intrinsic growth rates also affect dynamics, having a bigger impact on the assemblages lacking stabilization entirely. This showcases the robustness of stabilized assemblages against other dynamical forces, in contrast with the susceptibility of neutral dynamics. On the other hand, those species differences have a qualitatively similar impact on persistence times as niche differences: most species go out fast while a few last indefinitely. Moreover, high immigration blurs the dynamical differences between stabilized and non-stabilized communities. We conclude that niche differentiation can raise or reduce richness, persistence, and extinction, depending

on a series of factors examined in this study, and the effect is qualitatively similar to other types of species differences. It follows that these indices alone cannot distinguish between neutral and partially stabilized dynamics, unless one knows sufficient details about the community of interest to parametrize the niche model.

We note that the niche axis in our model is finite and carries edge effects. Although some modelers use circular axes to avoid this, a finite linear axis is arguably more realistic. In a highly symmetric case like our Baseline scenario where the only differences between species are niche differences, circularity drastically dampens the influence of niches on persistence times (Appendix S2: Fig. S6). This is because the positions of the niches on a finite axis are set, whereas on a circular axis they constantly shift through time, thus mitigating the effects of stabilization. However if other asymmetries occur, such as differences in regional abundances, the effect of circularity disappears (Appendix S2: Fig. S7), making the choice of a finite or circular axis inconsequential. Also, for the reader interested in the common choice of exponent 2 as opposed to 4 in the competition coefficients A_{ij}, we show in the supporting information (Appendix S2: Fig. S8) that the persistence time distribution in that model is much closer to neutrality (even on a finite axis). This is not surprising given the slower and weaker exclusion dynamics.

Our niche model shows a distinctive pattern of abundances by traits, mirrored by a similar pattern of persistence times: species are organized in clusters and separated by gaps; those at the center of the clusters are the residents and those at the gaps are the shortest-living transients. Each cluster is a group of species competing for the same niche, and in the absence of immigration only one species remains in each niche. Clusters are a recent extension of classical ideas of limiting similarity (MacArthur and Levins 1967, Holt 2006, Scheffer and van Nes 2006, Pigolotti and Cencini 2013). Fort et al. (2009) showed mathematically that they arise as a transient state on any deterministic niche model with a circular axis and competition tied to species similarity. Our model is similar but adds demographic stochasticity, immigration, and a finite axis. Clusters have been seen under these circumstances before (Barabás et al. 2013), and we recently proposed that they are a general outcome of niche-axis models (D'Andrea and Ostling 2016).

Note that while not all species have enhanced persistence under partial stabilization, the number of species that do is higher than the number of niches. In other words, it is not the case that only those species with a niche have enhanced persistence relative to neutrality. As we emphasized, the particular number will depend on immigration, regional abundances, environmental filters, and the map between species traits and degree of competition.

In our study we did not account for temporal changes in environmental conditions which may affect competitive interactions and intrinsic growth rates. Environmental

stochasticity in neutral models has been recently shown to be an important driver of species abundances (Chisholm et al. 2014, Kalyuzhny et al. 2015), and therefore presumably also of persistence times. It would be an interesting next step to test its effects on stabilized assemblages.

Our results are compatible with real-life observations of "core" species that persist for long times and "occasional" populations that regularly undergo local extinction and recolonization events. Magurran and Henderson (2003) found that occasional species in their study typically had different habitat requirements than core species, which suggest their differences in persistence arise from filtering effects analogous to Variants 3 and 4 in our model (Fig. 2C). However, the division between core and occasional species they find does not line up exactly with habitat requirements. This could occur under either neutral or niche dynamics. Core species may last longer simply by virtue of having higher regional and local abundance, but our results show how they could also be the beneficiaries of niche stabilization.

Upon finding that the estimated levels of immigration on Barro Colorado Island are compatible with neutrality given its observed richness, Condit et al. (2012) wrote that "species interactions, niche partitioning, or density-dependence, while they may be present, do not appear to enhance tree species richness at Barro Colorado." Our findings confirm that the connection between immigration and resulting richness is not unique to process, implying that Condit et al.'s observations are potentially also compatible with niche differentiation, and indeed that it is possible for niche partitioning to be present while not enhancing richness.

In general, insight into whether persistence dynamics are shaped by niches in nature will require more extensive data than collected by Magurran and Henderson (2003) or Condit et al. (2012). Inferring niches from species persistence is only rigorous when one can tease apart the effect of trait differences from the effect of regional and local abundances.

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Supporting Information