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RESEARCH ARTICLE

Functional Ecology

Vacant yet invasible niches in forest community assembly

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Abstract

1. It is controversial whether communities are saturated with species, or have vacant niches. The prevalence of vacant niches and the processes likely to promote their existence are poorly known.
2. We used a process-based forest gap-model to simulate plant community dynamics in 11 sites along a climatic gradient across central Europe. We then used hypervolume analyses to study the existence of vacant niches (seen as empty volumes in the trait space of local species pools and communities), and we tested for the effect of abiotic (environmental filtering) and biotic (competition) processes on the functional hypervolumes along the climatic gradient. Last, we performed invasion simulations to assess the invasibility of detected vacant niches.
3. Our results suggest that empty volumes in trait space are common, can arise from both abiotic and biotic processes and are more likely in cold climates. We also showed that most vacant niches are invasible.
4. *Synthesis*. Our work supports the view that niche space is unsaturated, and that many viable ecological strategies are absent from these forest communities.

KEYWORDS

assembly mechanisms, forest, functional traits, hypervolume, non-equilibrium, saturation, trait space

1 | INTRODUCTION

Are ecological communities saturated with species (Ricklefs, 1987)? This question is linked to whether ecosystems can reach equilibrium (Rohde, 2006), and whether introduced species are likely to invade ecosystems (Herbold & Moyle, 1986; Moles, Gruber, & Bonser, 2009). If a community is saturated, then the multidimensional niche space (i.e. the resources available and used by organisms), or 'hypervolume' [sensu Hutchinson] is filled with species (Harpole & Tilman, 2007). The 'classical' view of ecology has historically assumed that niche space is largely saturated, with biotic interactions (e.g. competition) promoting species packing and limiting the existence of empty volumes in the niche space. Conversely, the paradigm of 'non-equilibrium' ecology assumes that niche spaces are generally not saturated (Rohde, 2006). This view predicts a widespread occurrence of vacant niches in communities, where numerous empty volumes in niche space represent successful ecological strategies absent from the community. Identifying the causes and the nature of vacant niches is crucial for understanding community saturation (Harmon & Harrison, 2015) and more generally for identifying processes driving community assembly (Abrams, 1983). However, the prevalence and the processes generating vacant niches remain poorly known (Chase & Leibold, 2004; Cornell & Lawton, 1992). Here, we aim to determine which processes can generate vacant niches in communities, under which conditions they arise and whether vacant niches represent viable ecological strategies.

Vacant niches can result from several community assembly processes (Figure 1), which are commonly viewed as being nested (Cornell & Harrison, 2014). The species available to colonize a given site are determined by evolutionary diversification and biogeography

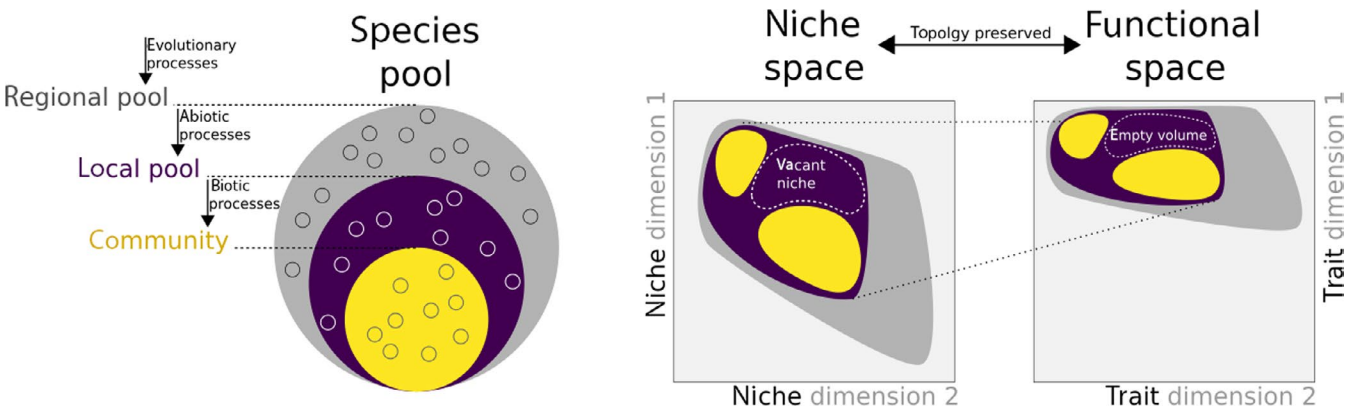

FIGURE 1 Nested assembly processes determine the community composition in terms of species pool (left), niche space (centre) and functional trait space (right). Community assembly processes can create vacant niches in niche space and empty volumes in functional space (white-dashed lines). The linkage between niche and functional space requires the following two assumptions: (i) functional traits related to ecological performance must be firmly linked to niche axes, such as the linkage between response traits and environmental conditions (e.g. temperature tolerance), demographic traits (e.g. growth rate) or traits linked to competition for resources (e.g. maximum height; D'Andrea & Ostling, 2016); and (ii) there must be a consistent mapping preserving the topology of trait and niche space across contexts. Linear and monotonic nonlinear relationships between traits and niche axes can satisfy this property. Note that this assumption might not hold under varying environment

(*regional species pool*). Abiotic processes determine a subset of species able to colonize and maintain viable populations under local abiotic conditions (*local species pool*). Biotic processes determine the subset of species able to maintain viable populations under abiotic and biotic conditions (*community*). Hence, a vacant volume in a community's niche space can result from any of these deterministic processes when they prevent the presence of well-adapted species in a given pool (Figure 1), or result from non-deterministic processes such as demographic stochasticity (Hubbel, 2001).

Classical niche approaches rely on the quantification of environmental factors that affect species performance. However, because of the complexity associated with the assessment of resource availability (Violle, Lecoeur, & Navas, 2007) and the identification of multiple co-limiting environmental factors (McGill, Enquist, Weiher, & Westoby, 2006), this quantification is particularly challenging and rarely achieved (Pulliam, 2000). A trait-based method, in contrast, does not require information on environmental factors, and has proven useful to quantify species niches along environmental gradients (Violle & Jiang, 2009; Violle, Reich, Pacala, Enquist, & Kattge, 2014). Moreover, the trait-based view of community ecology (McGill et al., 2006) provides a link with the niche, and a way to understand and predict how biotic and abiotic processes determine community assembly (Weiher et al., 2011). While the link between species niches and functional traits is a central assumption of trait-based community ecology, it is not strongly supported by empirical evidence because it can be modulated by environmental conditions (Adler et al., 2012; Angert, Huxman, Chesson, & Venable, 2009; Pérez-Ramos, Matías, Gómez-Aparicio, & Godoy, 2019). If we assume a consistent mapping between traits and niche axes under stable environmental conditions, recasting community assembly using trait (i.e. Eltonian niche, Elton, 1927) instead of environmental (i.e. Grinnellian niche, Grinnell, 1917) space provides an effective approach to the study of vacant niches (Figure 1). Vacant niches can then be assessed via the detection of empty volumes in community multidimensional functional space (i.e. a hypervolume).

An empty volume is operationally defined as a subset of the n-dimensional functional space that could be occupied, but is not. While the prevailing terminology has used the word 'holes', implying that the empty volumes are interior, this definition more inclusively allows for exterior empty volumes, that is, 'dents'. To date, only two studies (Alves & Hernández, 2019; Blonder, 2016) have measured empty functional space. The interpretation of observed patterns has remained unclear, especially in high dimensions where empty regions can be difficult to conceptualize or visualize (Blonder, 2016).

Trait-based ecology provides a valuable approach to understand how assembly mechanisms shape community composition, but the independent effects of multiple assembly processes are difficult to disentangle (Kraft et al., 2015; Mayfield & Levine, 2010; Srivastava, 1999). Thus, empirical results are often challenging to interpret due to the multitude of processes that can lead to the same pattern (Connolly, Keith, Colwell, & Rahbek, 2017). In contrast, process-based models provide a rigorous framework to understand the consequences of community assembly processes on functional space. Simulated community dynamics can directly arise from the interaction between the functional traits of the species and assembly mechanisms, enabling us to 'turn on or off' the effect of abiotic processes and/or biotic processes. While simulating species assembly often relies on simple (neutral) models (e.g. Hardy, 2008) or use of a priori linear relationships between traits and abiotic/biotic processes (e.g. Kraft, Cornwell, Webb, & Ackerly, 2007), process-based models avoid the circularity inherent to models based on explicit incorporation of assembly processes (Chauvet, Kunstler, Roy, & Morin, 2017; Falster, Brännström, Westoby, & Dieckmann, 2017; Herben & Goldberg, 2014). In process-based models, community assembly emerges from physiological mechanisms of environmental stress responses and competition for resources.

A set of traits define the individual's maximum growth rate, which is then modulated by local environmental conditions. Intra and interspecific interactions are not hardcoded, and biotic processes emerge from the difference between individuals' traits under varying environmental conditions via several negative feedback loops.

We used a process-based model to run empirically parameterized simulations of long-term (2,000 years) forest community dynamics in 11 sites with contrasting environmental conditions (Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011), and performed hypervolume computations to assess the presence of vacant niches as seen *via* empty volumes in the functional space (Figure 1). We then asked (Q1) which assembly processes could generate empty volumes, and (Q2) under which environmental conditions. While our simulations prevented testing predictions of the effect of evolutionary contingencies and dispersal limitation, we hypothesized that empty volumes could result from two different kinds of assembly processes. First, abiotic processes (i.e. environmental filtering, in our model) set aside species from the regional pool based on their trait values, and thus can generate an empty volume in the local pool functional space relative to the regional pool functional hypervolume. We predicted that the amount of environmentally filtered volumes would increase with environmental severity (e.g. climate extremes; Weiher, Clarke, & Keddy, 1998). Second, biotic processes (i.e. competition in this model) might generate empty volumes in the community relative to the local species pool. These empty volumes could be driven by multiple competition-linked processes present in the model, such as niche differentiation (D'Andrea & Ostling, 2016) and competitive-trait dominance (Smith & Huston, 1989; Tilman, 1987). For example, competition for light is likely to influence functional space via the segregation of individuals based on their maximum height. We also predicted that the amount of empty volumes in communities would increase with increasing environmental severity, as resource competition is expected to increase with resource availability and decrease with environmental stress (Bertness & Callaway, 1994).

Additionally, biotic processes might limit the invasibility of empty volumes in the community. That is, if empty volumes occur because of competition, then they may be non-invasible by species from outside the regional pool with suitable traits, leading to an inference that the community is saturated. Alternatively, if empty volumes are invasible, then the community is not saturated. An empty volume that cannot be invaded by a species with corresponding trait values and introduced at a low density could be identified as a non-viable ecological strategy. Conversely, an invasible empty volume would represent an absent, but viable strategy. We thus asked whether (Q3) empty volumes in functional space represented invasible strategies by performing invasion simulations. We expected that empty volumes generated from simulated forest communities could either represent invasible (positive growth rate following introduction) or non-invasible niche space (non-positive growth rate following introduction). Assessing the invasibility of vacant niches is an important step to move from pattern to prediction for vacant niche concepts in restoration and invasion ecology (Blonder, 2016). If vacant niches are generally invasible, then they could be used to predict the vulnerability of communities to invasion, as well as to predict which species may be most invasive based on functional traits. Similarly, better delineating empty niches might provide guidance for successful restoration approaches that focus on identifying native species with appropriate traits (Funk, Cleland, Suding, & Zavaleta, 2008).

2 | MATERIALS AND METHODS

2.1 | Simulating forest community dynamics

We simulated long-term temperate forest community dynamics using the forest gap model ForCEEPS (Forest Community Ecology and Ecosystem Processes; Morin et al., 2020). ForCEEPS is an individual-based model, relying on a minimum number of ecological assumptions (with few parameter requirements) to simulate forest dynamics in independent patches. Community-level outcomes emerge from context-dependent physiological mechanisms of environmental stress responses and assembly processes captured by the model. Abiotic and biotic factors determine tree establishment and growth, inter- and intraspecific competition, and changes in species composition. Individual-specific responses to winter temperature, light availability at the forest floor, growing degree days, soil moisture, nitrogen status and browsing pressure are defined by a set of functional traits. The main mechanism driving intra- and interspecific interactions is competition for light. Mortality is driven by both stochastic and deterministic processes depending on the following two components: (a) a 'background' mortality and (b) a stress-dependent mortality. Simulations were performed in 11 sites in Switzerland and Germany in which the model has been validated (Rasche, 2012). This set of sites covers a large productivity gradient related to elevation, temperature, precipitation and soil nitrogen. For each site, we ran simulations of forest dynamics for 2,000 years in 200 independent patches of 1/12 ha. The simulations were performed under stationary climate, without long-term trends, but with seasonal and inter-annual variation. This allows (a) to focus on the internal community dynamics and assembly processes, rather than the influence of environmental change; and (b) to respect the assumption of consistent mapping between trait and niche space which might not hold under varying environment (Adler et al., 2012; Angert et al., 2009; Pérez-Ramos et al., 2019). Each site is defined by baseline (climate and soil) conditions, and inter-annual variability (i.e. stability conditions) following the variability observed in these sites between 1901 and 1980 (Bantle, 1989). More details on the model, sites and species are provided in Appendix S1.

The regional pool was composed of the 30 most common tree species in Central Europe and was defined by 13 parameters that were estimated from a large body of literature data (see Appendix S2 and Bugmann, 1994). These parameters are considered as functional traits as they determine demography, physiological responses to environmental conditions, and intra- and interspecific competition outcomes, as well as take into account multi-trait trade-offs (Chauvet et al., 2017 and Appendix S2).

For each site, the *local pool* was defined as the set of species whose fundamental niche allowed successful establishment given

abiotic conditions, that is, in the absence of competition. Local pools were determined by performing single-species simulations for each of the 30 species at each site (Figure 2a). Following Chauvet et al. (2017), we defined a species as part of the local species pool if its biomass at the last time step of the single-species simulation was >0.01% of its best biomass in monocultures across the 11 study sites.

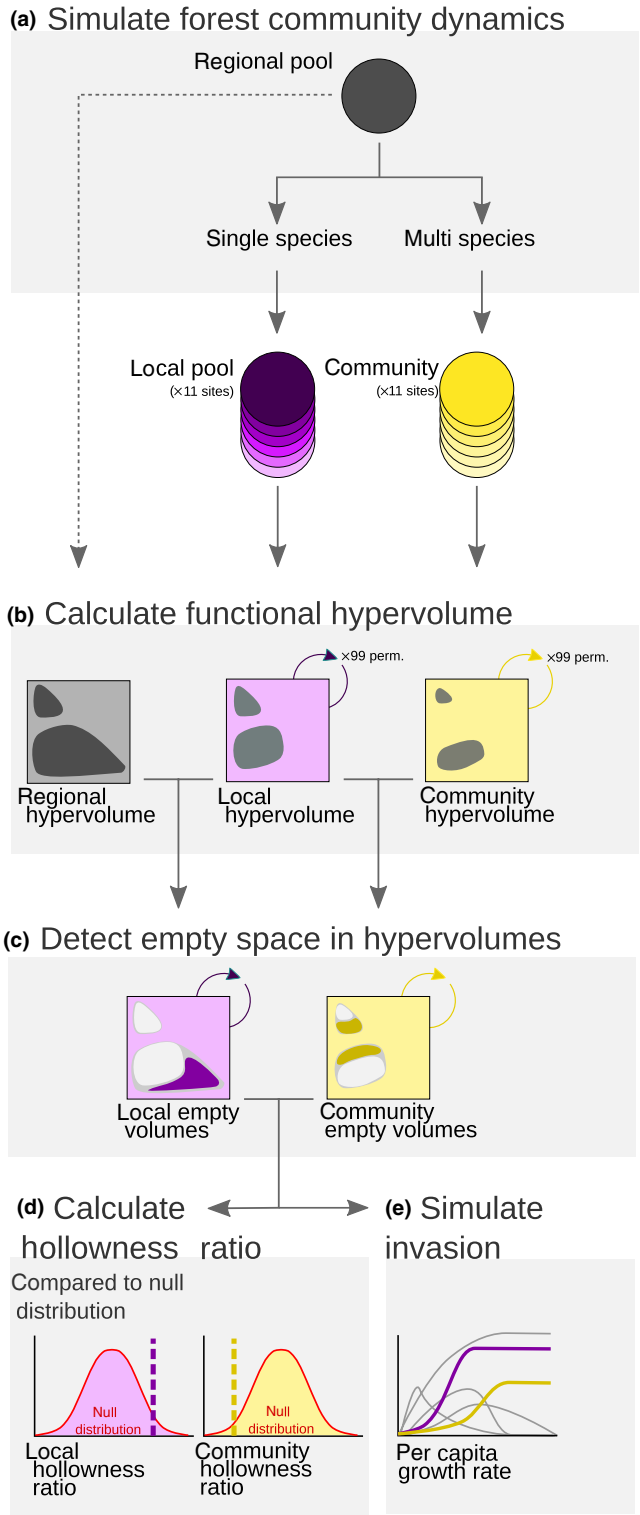

FIGURE 2 Data analysis workflow

For each site, the *community* was the set of species whose realized niche allowed successful coexistence under abiotic and biotic conditions. Communities were determined by performing mixed-species simulations at each site (Figure 2a). All species with species biomass representing more than 0.01% of the total biomass at the last time step of the simulation were considered part of the community (Chauvet et al., 2017).

2.2 | Functional traits and intraspecific variability

Among the 13 functional traits which determined responses to abiotic and biotic constraints in the model, we selected four traits to test for the effect of assembly processes on functional hypervolumes. We limited our analyses to four traits in order to meet guidelines for dimensionality versus sample size in hypervolume analyses (Blonder, Morrow, et al., 2018) and increase results interpretability. These four traits were related to species' environmental tolerances, growth and competitive ability. We specifically selected this set of four traits because they represent leading axes of variation, and have been previously identified as sensitive to biotic and/or abiotic assembly processes in this model (Chauvet et al., 2017). (a) Minimum annual degree day sum required for seedling establishment and growth (DDMin) determines the establishment and survival probability of individuals given abiotic conditions (i.e. temperature). (b) Maximum tree height (HMax) and (c) Shade tolerance (La) are important traits involved in resource exploitation and outcomes of biotic processes (i.e. competition for light). (d) Maximum growth rate (G) determines the optimal growth rate of individuals.

We also incorporated intraspecific trait variability (ITV) into these analyses (Violle et al., 2012). In the model, ITV can impact ecological dynamics via several mechanisms (Jensen's Inequality, Increased degree and Portfolio effect, see Bolnick et al., 2011), affect indirect interactions on community composition (Des Roches et al., 2018) and ultimately influence the topology of functional spaces (Albert et al., 2012). Adaptation of traits is not considered in the model that focuses on ecological processes. We assumed that the impact of trait adaptation on the community dynamics would not be of major importance for the considered time-scales, nor under stable climate. We modified the ForCEEPS model to incorporate ITV into simulations by defining an individual trait value randomly drawn from a given species' trait distribution for each seedling reaching a patch a given year (Appendix S1). ITV values were chosen to match realistic ranges of variation estimated from the empirical data used to parameterize the model (Bugmann, 1994).

2.3 | Quantifying empty volumes in the functional space

We used the workflow presented in Blonder (2016) and implemented in the HYPERVOLUME R package to calculate functional hypervolumes

(Figure 2b) and detect empty volumes (Figure 2c) for each species pool and site (one regional pool, 11 local pools, 11 communities). The calculation of hypervolumes follows a multidimensional kernel density estimation procedure (see Blonder, Lamanna, Violle, & Enquist, 2014 for a detailed description). We followed a standardized method (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016) to apply the same kernel bandwidth value, guaranteeing comparability between different hypervolumes. We retained a bandwidth value of 2 × the bandwidth value estimated using the cross-validation plug-in estimator (Blonder et al., 2014) on the regional species pool. This value was chosen based on the level of definition in the detection of hypervolumes and empty volumes (see Appendix S4). In order to calculate comparable hypervolumes between different pools independently from their sampling size, local hypervolumes were calculated with *n* observations randomly sampled from the total observations in the local pool, where *n* represents the number of individuals present in the community of each site.

To determine which assembly processes are likely to generate vacant niches (Q1), we calculated empty volumes created under abiotic and biotic processes separately (Figure 2b,c). Empty volumes created under abiotic processes were calculated as the set difference between the regional (pool) hypervolume and the local hypervolume (Figure 2b,c). Empty volumes created under biotic processes were calculated as the set difference between the local hypervolume and the community hypervolume (Figure 2b,c). Note that this procedure accounts for interior empty volumes (i.e. 'dents' and 'holes') but not exterior empty volumes beyond the regional pool of species considered (i.e. 'bumps').

If unspecified, the parameters used in all subsequent analyses were default parameters from package functions (hypervolume version 2.0.11). In the package, uniqueness was based on a distance factor of 1.5, a maximum of 20,000 random points was retained in the input, and all empty volumes represented by fewer than 20 random points were removed.

The hollowness ratio of the local pool (abiotic processes) was then calculated as the empty volume in the local pool divided by the volume of the regional hypervolume, ranging from 0 if the hypervolume is filled to 1 if the hypervolume is empty (Figure 2d). Similarly, the hollowness ratio of the community (biotic processes) was calculated as the empty volume in the community divided by the volume of the local hypervolume (Figure 2d). We also took into account the influence of random assembly processes on local and community hypervolumes by comparing hollowness ratios with the distributions of hollowness ratios obtained from null models (Figure 2d). Both local and community null models followed the null hypothesis that the distribution of trait values of individuals within a given pool is a random draw from a larger pool. The randomization procedure consisted of 99 draws of *n* individual trait values (without replacement) belonging to the larger pool. For each drawing, we ran all the previous analyses to build a null distribution for the local and community hollowness ratio.

To investigate the effect of abiotic conditions on empty volumes (Q2), we tested (for local pool and community scale separately) whether the hollowness ratios were related to the mean annual temperature (°C) of the site using linear models (hollowness ratio was the explained variable, regressed over the mean annual temperature of the site). We chose this environmental descriptor among others because it is clearly linked with the trait *Minimum annual degree day sum*. To further assess which trait dimensions were the most influenced by abiotic and biotic processes, and how empty volumes on each dimension were related to mean annual temperature, we also projected the empty volumes on each of the four trait axes and tested their relationship with mean annual temperature using linear models.

2.4 | Virtual invasion experiments

To determine if empty volumes in functional space represented invasible strategies (Q3), we created a virtual invader species for each unique empty volume detected in communities. For shade tolerance, minimum degree day sum, growth rate and maximum height, the invader's trait values were randomly drawn from a normal distribution with the mean trait value corresponding to the centroid of each detected empty volume. Standard deviation (*SD*) was defined as in Appendix S1. For the other traits not considered in hypervolume analyses, individual values were randomly drawn from a normal distribution with parameters corresponding to the community average trait mean value and *SD*. To account for the strong correlation between maximum age–maximum height and winter temperature-minimum degree day sum, the mean and *SD* for maximum age and winter temperature were respectively predicted from the linear relationship with maximum height and minimum degree day sum based on the regional pool individual values.

We first performed single-species simulations for each invader and their assigned site to test their ability to colonize (i.e. to pass through the environmental filter). We performed simulations with a starting community state corresponding to the final state of initial simulation (at t = 2,000 years), and a species pool corresponding to the initial simulation species pool (Appendix S2) plus the virtual invader defined for each community and each empty volume. Each simulation ran for 1,000 years under a stationary climate with seasonal and inter-annual variation. To determine invader success in both single-species and multi-species invasion simulations, we fitted a logistic growth model to the dynamic of the invader's total biomass using nonlinear least square models (function *nls* in R). From each model, we extracted the model fit (as the correlation coefficient between observed and predicted values), the estimated growth rate (r) and the asymptotic value (K) with associated standard error and p-value. We interpreted a significantly positive ($p < 0.05$) value of r over the 1,000-year simulation as a successful invasion (Grainger, Levine, & Gilbert, 2019). We also tested the invasibility of filled volumes in the functional space of each community. To do so, we used the same approach, with invader's trait values randomly drawn from a normal distribution with the mean trait value corresponding to the centroid of each detected filled volume, instead of empty ones.

3 | RESULTS

Hollowness ratio values calculated from simulated pools (i.e. determined by assembly processes) were significantly different from the distributions of hollowness ratios (except for Sion) extracted from null models (Figure 3). Hollowness ratios ranged from 0 (Sion community) to 0.68 (Davos community). Both local and community pools had empty volumes. Local pool hollowness ratios were low compared to the community ones, ranging from 0.06 to 0.34 (0.15 ± 0.09 [mean ± *SD*]). Community hollowness ratios showed strong variability between sites with values ranging from 0 to 0.68 (0.42 ± 0.19 [mean ± *SD*]). The community in Sion was the only one without an empty volume.

Local pool and community hollowness ratios were negatively related to the monthly mean temperature of the site (Figure 4). The local pool hollowness ratio decreased with increasing temperature (linear model −0.025 ± 0.0036 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.83). The community hollowness ratio also significantly decreased with increasing temperature, although the relationship was less clear (linear model −0.044 ± 0.014 [estimate ± *SE*], *p*-value = 0.012, adj. r^2 = 0.46). Hollowness ratios were not significantly related to other environmental variables (annual precipitation, soil nitrogen content, maximum productivity).

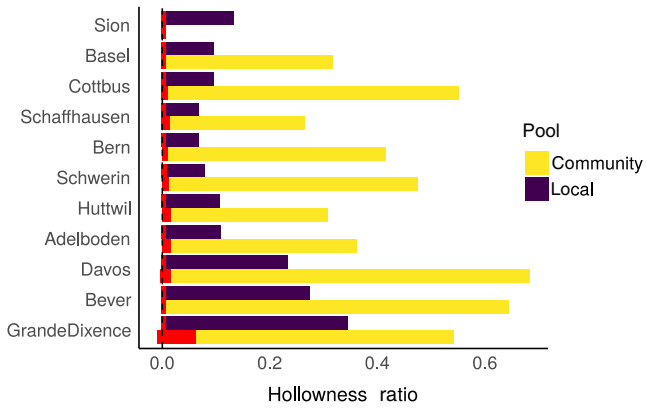

FIGURE 3 Hollowness ratio per site for local pool (yellow) and community (purple). Sites are arranged from warmest (Sion) to coldest (Grande Dixence) conditions. Red bars show the lower and upper 95% confidence intervals of the null distribution of the hollowness ratio

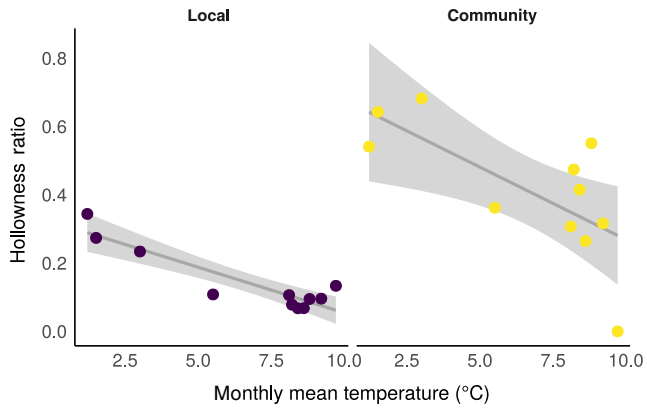

FIGURE 4 Linear model relationships between hollowness ratio and monthly mean temperature for local pool (purple) and community (yellow). Grey lines show linear model slopes with associated standard error (grey-shaded area)

Projecting local pool empty volumes on the different trait axes (Appendix S5a) showed that empty volumes were predominantly situated in strong shade tolerance (for cold sites 4.7 ± 2.78 degree days [mean ± *SD*], low values correspond to strongest tolerance) and were not related to the mean temperature of the sites (Appendix S5b). Local pool empty volumes were situated in high minimum degree day sum values (for cold sites, 986 ± 259 degree days [mean ± *SD*]), and were negatively related to the mean temperature of the sites (Appendix S5, linear model −68 ± 1.3 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.35). Along the growth rate dimension, local empty volumes were situated in low values (for cold sites, 154 ± 71 [mean ± *SD*]) and were positively related to the mean temperature of the sites (Appendix S5, linear model 17 ± 0.57 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.16). Along the maximum height dimension, local pool empty volumes were normally distributed and centred along the axis (for cold sites, 33.9 ± 14.7 m) and were not related to the mean temperature of the sites (Appendix S5).

Projecting the community pool empty volumes showed that they were predominantly situated in high shade tolerance values (7.51 ± 1.96) and were negatively related to the mean temperature of the sites (Appendix S5, linear model 0.089 ± 0.007 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.021). Along the minimum degree day sum dimension, empty volumes were predominantly situated in low values (587 ± 260 degree days) and were positively related to the mean temperature of the sites (Appendix S5, linear model 30 ± 0.8 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.14). Along the growth rate dimension, empty volumes situated in the cold sites showed a bimodal distribution peaking at low (<300) and high (>500) values. In other sites, empty volumes were preferentially distributed in low values (monthly mean temperature > 5°C, 169 ± 87 [mean ± *SD*]). Overall, empty volumes were negatively related to the mean site temperature (Appendix S5, linear model −16.4 ± 0.44 [estimate ± *SE*], *p*-value < 0.001, adj. r^2 = 0.154). Along the maximum height dimension, empty volumes were predominantly situated in low values (for all sites 26.9 ± 14.9 metres [mean ± *SD*]) and were not related to the mean site temperature (Appendix S5).

In invasion simulations, all invaders representing species with traits characteristic of these empty volumes were able to colonize in the absence of competition (i.e. in single-species simulations), except for the second invader in Bever (Figure 5). Additionally, all invasion simulations showed a significantly positive per capita growth rate for all invaders in the presence of competition. Logistic model fits were generally high (correlation coefficient between predicted and observed values >0.8), except for Grande Dixence 2 (cor = 0.58) and Davos 2 (cor = 0.65). Per capita growth rates ranged from 0.013 (Schwerin 1) to 0.138 (Davos; Figure 5). Per capita growth rates from multi-species simulations were generally lower than single-species

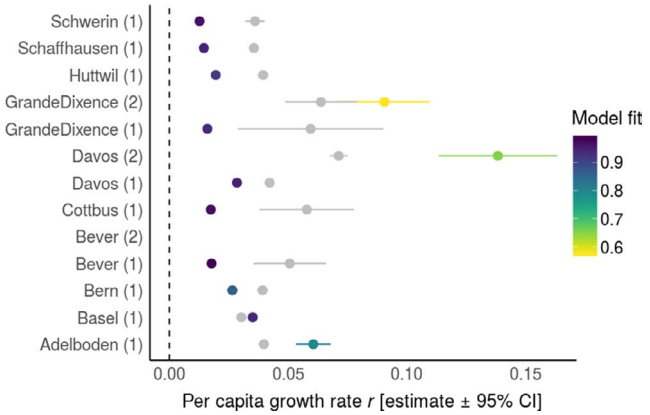

FIGURE 5 Per capita growth rate (estimate ± 95% CI) estimated from the logistic growth model. Invader names (*y*-axis) correspond to the site name and the empty volume number (1 or 2). Coloured points show the per capita growth rate value in multi-species invasion simulations. Grey points show per capita growth rate when the invader is introduced alone in the site

ones, except for Grande Dixence 1 and 2, Davos 2 and Adelboden 1. Detailed model outputs are shown in Appendix S6.

In invasion simulations based on filled volumes, all invaders had a significantly positive per capita growth rate, with the exception of at Cottbus (see Appendix S7). However, per capita growth rates of invaders with a set of traits corresponding to filled volumes were lower than the per capita growth rates of invaders with sets of traits corresponding to empty volumes for all communities, except Schwerin (see Appendix S7).

4 | DISCUSSION

4.1 | Assembly processes generate non-saturated functional space

We found empty volumes in functional space at almost all the sites and scales, suggesting that vacant niches are common in realistically simulated communities. This result supports the idea that unsaturated communities might be common, an observation in line with theoretical work suggesting a high prevalence of vacant niches (Rohde, 2005). We showed that empty volumes resulted from the interplay between environmental constraints on the establishment and growth of individuals, and the inter- and intraspecific competition between those individuals. Our results further showed that the effect of biotic processes was stronger and more variable than abiotic processes in promoting empty volumes, as shown by the higher hollowness ratios found in communities when compared to local pools. When considering abiotic processes alone, empty volumes were generally detected at the periphery of the hypervolumes (see Appendices S5 and S8). This is in line with a previous simulation study (Chauvet et al., 2017) and with the idea that environmental filtering reduces trait variability (Cornwell, Schwilk, & Ackerly, 2006; Grime, 2006). However, empty volumes generated by biotic processes were also detected within hypervolumes rather than at the periphery (Appendix S8). This suggests that low dimensional space analyses based on convergence or divergence in trait distributions might limit the inference drawn from the study of community functional spaces. Conventional approaches for the analysis of functional community composition relying on the community-weighted mean and variance (Sonnier, Shipley, & Navas, 2010), or functional space descriptors such as functional dispersion or divergence (Villéger, Mason, & Mouillot, 2008) could obscure complexity in multidimensional distributions, leading to unclear and idiosyncratic patterns which are sometimes difficult to interpret (e.g. Bernard-Verdier et al., 2012; Chauvet et al., 2017; Götzenberger et al., 2012). Here, we demonstrated that the study of empty volumes in the functional space of a community can provide a fine assessment of how assembly processes affect community composition and structure.

4.2 | Abiotic conditions influence saturation of functional space

Linking the amount of empty volumes detected in the functional space with the temperature of each site showed that the effect of both abiotic and biotic processes varied with local environmental conditions. The amount of empty volumes in the local pool decreased with increasing temperature, supporting our prediction that colder climates promote the presence of vacant niches via stronger environmental filtering based on species traits. Our study was limited to temperate and montane climates, in which the 'extreme' climatic boundaries are situated in the coldest conditions (given the regional species pool). The amount of empty volumes in communities tended to decrease with increasing site temperature. This result falsifies our prediction of a stronger effect of competition under warm conditions as predicted by the stress gradient hypothesis (Bertness & Callaway, 1994). However, the effect of biotic processes was still closely related to the abiotic context, which challenges the common view of community assembly as sequential and independent filters (Kraft et al., 2015). Instead, it supports the idea that the effect of biotic interactions on community assembly varies with abiotic conditions, as suggested by recent theoretical and empirical studies (Bimler, Stouffer, Lai, & Mayfield, 2018; Germain, Mayfield, & Gilbert, 2018).

Surprisingly, hollowness ratios were not related (or only weakly related) to other environmental variables (e.g. annual precipitation, drought index, nitrogen soil content). This is likely due to the limited amount—and the choice—of functional traits used in the analyses, as well as the range of environmental conditions. The main environmental-response trait integrated in our analyses was the minimum annual degree day sum required for seedling establishment and growth, a choice based on a previous study showing the importance of this trait in structuring functional composition in the same sites (Chauvet et al., 2017), and in line with the key role of temperature in determining species distribution and community dynamics in European forests (Sykes & Prentice, 1996).

Projecting the hollow volumes on the different trait dimensions allowed for a finer interpretation of the effect of different assembly processes on functional traits. In the local pools, the *Minimum annual degree day sum*, the *Maximum growth rate* and the *Shade tolerance* of plants appeared to act as determinant functional traits linked with vacant niches. Local empty volumes for the 'cold' sites (Grande Dixence, Bever, Davos) displayed a unimodal distribution skewed towards high minimum degree days, low shade tolerance and low growth rate. For the warmer sites, distributions were generally bimodal along *Growth rate* and *Maximum height* with values distributed in low and high values. This bimodality indicates that two distinct empty volumes in local species pools were promoted by thermal conditions filtering out individuals poorly adapted to cold conditions, with high shade tolerance and growth rate (e.g. *Pinus uncinata*). When considering all sites, the *Minimum annual degree day sum* and the *Maximum growth rate* were related to the annual mean temperature of the site, showing that these functional traits are the most determinant for environmental filtering based on temperature. In communities, the positions of empty volumes were constrained along all functional trait axes, but their distributions varied between sites in relation to annual mean temperature. Competition for light predominantly filtered out individuals with low shade tolerance, high growth rates and low maximum height. This process was linked with site thermal conditions along two trait dimensions: the Minimum annual degree day and the Maximum growth rate. Note that (a) these results emerge from physiological mechanisms of environmental stress responses and competition for resources, and are not obvious outcomes of the simulations as our model does not explicitly incorporate assembly processes; (b) different levels of ITV might influence these results, as lower ITV tends to increase the absolute hollowness of hypervolume (and conversely for higher ITV). However, we can expect the influence of ITV on absolute hollowness to be consistent across pools and sites. In this case, the hollowness ratio should not be strongly affected by variation of ITV levels.

4.3 | Empty volumes are invasible

Invasion simulations revealed that almost all unique empty volumes detected in communities were invasible. When introduced at low density in the resident community, almost all invaders had a significantly positive per capita growth rate. This result supports the idea that unsaturated niche spaces contain ecologically viable strategies which are not presently occupied. In turn, this interpretation suggests that newly evolved or non-native species could colonize a community if they were to have a set of traits corresponding to a vacant niche.

We also found that the filled volumes in community functional spaces were also invasible, although the realized per capita growth rate of invaders and the size of the populations at pseudo-equilibrium were consistently lower compared to those of invaders in empty volumes. Moreover, the high density of individuals in filled volumes appears to limit the population expansion of invaders in filled volumes more than in empty volumes. Although such interpretation would require a deeper investigation which is out of the scope of our study, it supports the idea that communities are largely unsaturated, but also that vacant niches represent particularly favourable opportunities for potential invaders.

Because our study focused on the ecological processes likely to generate vacant niches, we limited invasion analyses to volumes in the functional space that were generated from well-identified assembly processes. Thus, our invasion analyses do not pretend to assess the invasibility of the entire community functional space, but only the invasibility of the vacant niches generated by abiotic and biotic assembly processes. It is likely that areas of the trait space not tested here would be invasible, for several reasons. First, the regional pool of 30 species hard-coded in the model only contains the main dominant species in such ecosystems, hence not representing the diversity of ecological strategies present in the 'real' regional pool of these sites. Secondly, we only considered vacant niches as dents and holes compared to the regional or local functional space. While it is likely that empty volumes falling outside the regional pool functional space might be invasible, it is also impossible to assess their ecological or evolutionary realism.

Our results support the idea that invasion from alien species might occur when species have traits enabling them to exploit vacant niches in communities (Thompson & Davis, 2011). The question of the invasibility of empty volumes needs deeper investigation independent from the mechanisms implemented in ForCEEPS. Despite these limitations, we argue that, in line with recent studies exploring the integration of community assembly theory and functional ecology into invasion biology (Lenzner et al., 2019; Pearson, Ortega, Eren, & Hierro, 2018), the detection and characterization of empty volumes in functional space is a promising tool to predict the invasibility of plant communities.

5 | CONCLUSIONS

Our study supports the view that niche space is largely unsaturated, even in static environments. However, our simulations relying on empirically parameterized sites situated in central Europe—an area with a recent glaciation history—are more likely to show unsaturation of niche space than other biogeographic ecozones such as the Neotropics (Blonder, Enquist, et al., 2018; Ordonez & Svenning, 2016). Further investigations on the prevalence of vacant niches in diverse biogeographic contexts are needed to generalize and extend our findings. Another promising development of our work lies in testing the effect of climatic variation (long-term change in climate and extreme events such as drought and cold winters) on the saturation of communities' functional space in time. Regardless, we showed that vacant niches can represent viable ecological strategies absent from the community, and might provide successful invasion opportunities for species with corresponding sets of traits. This perspective

is in line with abundant empirical evidence (Cornell, 1999; Gotelli & Rohde, 2002; Lekevičius, 2009) and supports disequilibrium perspectives (Rohde, 2006; Svenning & Sandel, 2013).

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AUTHORS' CONTRIBUTIONS

P.G. led the study; P.G. and B.B. conceived the ideas; X.M. conceived the model; B.B. created the HYPERVOLUME package; P.G. and X.M. performed the simulations; P.G. and I.C. analysed the data; P.G. wrote the first draft of the manuscript. All authors contributed substantially to the writing.

DATA AVAILABILITY STATEMENT

Data and code to replicate the results of the study are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.vx0k6djp4 (Gauzere et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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