

Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns

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Abstract Intra-specific variability often produces an overlap between species distributions of individual performances which can influence competition relations and community dynamics. We analysed a two-species competition–colonisation model of vegetation with intra-specific variability in juvenile growth. On each patch colonised by both species, the winner was the juvenile with higher individual growth. Intra-specific variability disproportionately favoured the more fecund species because the tail of its distribution represented more individuals. In some cases, this process could even lead to a reversal of competition hierarchy and exclusion of the species with higher mean juvenile performance. In the space of species

2 mean growth and fecundity traits, the combinations of traits allowing coexistence with species 1 appeared close to an ideal trade-off curve. Along this curve, species 2 and species 1 coexisted at similar abundance. The balance of relative abundances diminished with the distance of species 2 from this curve. For a given level of relative species performances, coexistence stability increased continuously as species differentiation increased. In contrast to classical models that exhibit abrupt changes of equilibrium community properties when species traits vary, our model displayed continuous changes of these properties in relation to the balance of life traits within and among species. Intra-specific variability allows flexible patterns of community dynamics and could explain discrepancies between observations and classical theories.

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Introduction

Species differences in life history traits have been recognised as a key to species relative fitness, community structure and species coexistence (Amarasekare et al. 2004; Cordonnier et al. 2006; Kneitel and Chase 2004; Leibold et al. 2004; Rees et al. 2001). The classical niche theory states that differences between species can lead either to competitive exclusion or to niche partitioning, depending on whether the advantages conferred by one trait are balance by a trade-off on another trait or not (Chesson 2000b; Leibold 1995; Sivertown 2004). When species coexist, differences in traits determine also species relative abundance (Kinzig et al. 1999) and community stability (Kinzig et al. 1999; Adler et al. 2007).

Species differences and tradeoffs are usually analysed in terms of mean population trait values. However, recent advances in statistical methods have shown that intra-specific variability can be large and produce an overlap between the distributions of individual performances among species (Chave 2004; Clark et al. 2007; Clark et al. 2004; Clark et al. 2003; Lichstein et al. 2007; Mason et al. 2008). For instance, Clark et al. have shown that in mixed forests of North Carolina, the overlap between distributions of *Acer rubrum* and *Liriodendrum tulipifera* sapling growth performance was very high for all levels of light (Clark et al. 2004). In a statistical context, intra-specific variability is best described by individual effects that characterise differences between individual and mean population responses that are persistent during the time period covered by a data set. In practice, statistical mixed models allow separate individual effects from other variability terms if several observations through time are available for each individual (Clark 2007; Frees 2004). In contrast, temporal effects characterise the variations of performance between years common to all individuals, and noise terms represent unstructured remaining variations. Individual effects can be related to factors such as genetic variability, past biotic interactions or small environmental variations that are usually unmeasured or not measurable and then discarded in ecological studies. In simulation models, individual effects can be drawn at the beginning of an individual's life in distributions inferred from data. The same effects are then applied to this individual every time step of its life.

Recent studies have discussed the effect of intra-specific variability on species coexistence, expressing contrasting views. Clark et al. (2003, 2007, 2010) has argued that tradeoffs between mean species traits are usually weak. They will rarely predict coexistence when parameter estimates are plugged into theoretical models. However, variations among individuals allow species to differ in their distributions of responses to the environment. Relations between performance parameters at the individual level change also from one species to the other. Intra-specific variations can then lead to subtle niche differences. Despite little differences between species mean responses, correlation between individual responses to environmental variations appear stronger within a species than among species, leading potentially to stronger intra-specific than inter-specific competition and favouring coexistence (Clark 2010, Clark et al. 2010).

Lichstein et al. (2007 #1466) emphasised another outcome of intra-specific variations: the overlap between species distributions of performance, and its consequences on the probability that the single best individual winning a site belong to one species or the other. When species distributions overlapped completely, the potential of both species was the same, community dynamics was unpredictable and coexistence was unstable. Depending on the level

of overlap, a gradient between stable and unstable coexistence arose. Lichstein et al. (2007 #1466) studied the special case when a species with lower mean performance had higher variance in individual performances. In that case, stable coexistence occurred for intermediate levels of competitor densities. However a mean-variance trade-off is probably difficult to find in nature where mean and variance are often positively correlated. Moreover, the effect was strong only at very low densities.

The effect of density detected by Lichstein et al. (2007 #1466) calls for a closer look at a potential interaction between intra-specific variability and fecundity. First, Lichstein et al. have studied only cases where both species had a same fecundity, whereas species differences of fecundity can be assumed in most communities. Second, the analysis of the effect of intra-specific variability on community structure and dynamics should not be limited to the question of coexistence alone, but should also include potential effects on competition hierarchy, species abundance and community stability.

In this work, we focused on the potential interactions of intra-specific variability with differences of fecundity and mean competitive ability. We used a two-species patch model where juvenile competition on a patch depended on seedling growth, drawn on distributions corresponding to their species. We used parameters within the order of magnitude of observations of juvenile production, mean growth and growth variability for the forest tree species *Abies alba*, *Picea abies* and *Fagus sylvatica*.

Our objective was to analyse how intra-specific variability would change the combinations of mean traits allowing a pair of species to coexist, and the characteristics of coexistence. We examined the following questions: Would intra-specific variability modify the range of traits allowing species to coexist, or only shift the trade-off between mean traits required for coexistence? Would it favour species with high fecundity or species with high mean growth? Would it modify coexistence stability and relative species abundance? How would species similarity influence their coexistence?

We showed that intra-specific variability deeply modified the dynamics of a community. In the space of species traits, patterns of species hierarchy, coexistence, relative abundances and stability appeared in relation to the distance along and to a line representing an ideal trade-off allowing coexistence at similar abundances.

Model and method

A simulation model of vegetation community dynamics

A patch model of forest dynamics was developed for this study, in the lineage of the classical Levins meta-population

model (Hastings 1980; Levins and Culver 1971; Tilman 1994). Our model was based on space pre-emption by adult trees and local competition between seedlings on patches released by adult mortality. Analytical formulations of comparable models have been derived for an infinite number of patches in cases where there was no intra-specific variability in seedling competitive ability but imperfect inter-specific competition asymmetry (Kisdi and Geritz 2003) and in cases where seedling competitive abilities were distributed uniformly (Lichstein et al. 2007). Nevertheless, analytical analysis of these models is limited by their complexity, and previous authors needed simulations for a broader exploration of the models' behaviour. We present here only a simulation approach for a finite number of patches. The dimensions of a patch corresponded to the dimensions of an adult tree. Time was discrete in the model and a time step corresponded to the time required for a seed to become an adult tree.

The number of adults $N_{s,t+1}$ of species s at time $t+1$ depended on adults at time t , $N_{s,t}$, mortality $M_{s,t}$ and recruitment of new adults $R_{s,t}$:

$$N_{s,t+1} = N_{s,t} - M_{s,t} + R_{s,t}$$

Mortality was drawn in a binomial distribution with the parameters being the previous number of adults and the probability of dying m_s

$$M_{s,t} \sim \text{Binom}(N_{s,t}, m_s)$$

The number of juveniles produced by each adult was f_s , resulting in a total number of juveniles $f_s N_{s,t}$. Dispersal across the landscape was random. With P the number of patches, the probability for a juvenile to fall on any patch was $1/P$ and the P -length vector of probabilities of falling on every patch was $[1/P]$.

The P -length vector giving the number of juveniles on every patch was drawn in a multinomial distribution

$$[J_{s,p,t}] \sim \text{multinom}(f_s N_{s,t}, [1/P])$$

Juveniles fallen on patches already occupied by adults died. The subset of patches without adult was examined for competition among juveniles and recruitment.

The competitive ability of juvenile i of species s was associated to its initial height growth $g_{i,s}$. This growth was drawn in a lognormal distribution with mean and standard deviation depending on the species.

$$\log(g_{is}) \sim N(m_s, \sigma_s)$$

Competition for light is highly size-asymmetric in a forest and we considered that the local hierarchy between saplings was stable during the juvenile phase and was determined by initial differences of height growth. The juvenile with highest growth was identified on each patch.

Recruitment of species s on patch p was 1 if the best juvenile on that patch belong to species s or 0 if there was no juvenile of this species on the patch or if a juvenile from another species was more competitive. Recruitment for species s on every patch was synthesised in the P -length vector $[R_{s,p,t}]$. The number of adults of species s recruited $R_{s,t}$ was

$$R_{s,t} = \text{sum}([R_{s,p,t}])$$

In this model, the juvenile stage was collapsed to a single time step. The hierarchy between seedlings on a patch was determined by a single draw of their initial increment. As this hierarchy was not modified by subsequent draws, the differences between individuals were permanent, not transient. These effects were then considered as comparable to individual effects (the permanent part of the differences between individuals in a statistical context). The overlap between species juvenile competitive abilities, which was not reversed by subsequent events, led to imperfect competition asymmetry as in a weighted lottery model and to various competition outcomes at the end of the juvenile phase.

Parameters

To work in a realistic framework, we evaluated fecundity and seedling relative height growth from the literature for three coexisting tree species in European forests: European fir (*A. alba*), European beech (*F. sylvatica*) and Norway spruce (*P. abies*). As we lacked a complete set of parameters estimated in a single forest over a long time period, these parameters can only be considered as orders of magnitude. We arbitrarily fixed adult tree diameter at breast height to 40 cm. Basal area allowed evaluate seed production for the three species (Mencuccini et al. 1995; Sagnard et al. 2007). We multiplied fecundities by emergence rates (Sagnard et al. 2007; Vanderberghe et al. 2006) and first year survival (Vanderberghe et al. 2006) and obtained a production of 2-year seedlings of 23.03, 28.83 and 497.13 seedlings/adult/year for fir, beech and spruce, respectively (i.e. log-fecundities of 3.14, 3.36 and 6.21, respectively). We considered competition among seedlings belonging to the first cohort settling on a patch. Competition was determined by the seedlings' relative height growth.

We evaluated sapling height growth mean and variability from the data set of Stancioiu and O'Hara (2006), who analysed sapling relative height growth (annual height increment/height) as a function of light for our three species. We restricted their data to situations with less than 40% above canopy light, i.e. a relatively closed forest with small gaps. We evaluated mean log-relative height growth at 2.30, 2.25 and 1.68 for fir, beech and spruce, respective-

ly. The mean standard deviation of log-relative height growth for the three species was 0.5. Given the scale of their study, the standard deviation of sapling growth represented individual variations due both to genetic differences within a species and small local heterogeneity of environmental conditions. The heritable component of this variability was difficult to evaluate and we considered it as not heritable in this first approach.

Simulation design

We ran two-species community simulation experiments to analyse the impact of species fecundity and mean seedling growth on species coexistence, either with or without intra-specific variability in seedling growth. In each experiment, we fixed fecundity and mean growth of a reference species (species 1) and varied parameters for the other species (species 2). We then analysed the results of community dynamics in the parameter space of species 2.

For each combination of parameters, we simulated communities of 500 patches over 500 time steps, with a mortality rate of 0.1 deaths/adult/time step for both species. We made five simulations for each combination of parameters with initial abundances of, respectively, 10%, 30%, 50%, 70%, 90% for species 1 and 90%, 70%, 50%, 30%, 10% for species 2. We assumed that a species with initial abundances of 10% could be considered rare. We synthesised the results of an experiment in the parameter space of species 2, by points representing the combined result of each set of five simulations. We obtained four possible outcomes represented by different symbols: (1) exclusion of species 1 whatever the initial abundance, (2) exclusion of species 2 whatever the initial abundances, (3) coexistence of both species at the end of the simulation period whatever the initial abundances and (4) undetermined result. This last category grouped cases where extinction of a species occurred for some replications and coexistence for other replications and cases where different species became extinct in different replications. Relative abundances at equilibrium were calculated in case of coexistence. In case of exclusion, the time before exclusion was calculated as the mode of the times before exclusion of the five simulations representing the same parameter combination. A time identical to the simulation time length (500 time steps) indicated that exclusion did not occur. A long exclusion time indicates that deterministic exclusion processes are weak compared to random drift processes. An equilibrium stability index was calculated as the time needed for convergence to equilibrium abundances of the five simulations starting from different initial relative abundances. Convergence was assumed when the standard deviation between abundances in the five simulations was less than 50% of the initial standard deviation. Fast

convergence indicated that rare species were well protected from exclusion by stabilising mechanisms, whereas slow convergence indicated that there was a risk of extinction of a rare species through random drift, a characteristic of unstable coexistence.

We used the parameters evaluated for European fir, Norway spruce and European beech to evaluate realistic parameter exploration ranges. We present first two experiments made on species with lower fecundity, which gave more general results, and a third experiment involving our three field species. In the first experiment, species 1 (the reference species), was a hypothetical species of intermediate growth (mean log-growth, 3) and intermediate fecundity (log-fecundity, 12). The mean growth and fecundity of species 2 varied within the parameter space (mean log-growth from 1.1 to 5 and log-fecundity from 0.2 to 8). This experiment was conducted without intra-specific variability: every seedling in the same species had the same growth rate (log-growth standard deviation, 0).

In the second experiment, species 1 was still a hypothetical species of intermediate mean growth (mean log-growth, 3) and intermediate fecundity (log-fecundity, 1.2), but this time, intra-specific variability was simulated by drawing seedling log-growth rates in normal distributions (log-growth standard deviation, 0.5 for both species).

In the third experiment, species 1 corresponded to European fir (mean log-growth, 2.3; log-fecundity, 3.14) and intra-specific variability was taken into account (seedling log-growth standard deviation, 0.5 for both species). Plotting European fir and Norway spruce in the parameter space of species 2 allowed us to analyse their possible coexistence with European fir. Detailed analysis of competition outcomes at the patch scale on contrasting simulation cases provided a detailed understanding of the processes leading to coexistence or exclusion.

Results

Patterns of coexistence

Figure 1a represents the results of the first simulation experiment (reference species of intermediate trait values, no intra-specific variability), in the parameter space of species 2. The point corresponding to the location of species 1 is pivotal in this figure. On the left side of the graph, species 2 had a lower growth rate than species 1. Species 2 was excluded when its fecundity was low (lower left quarter) and both species survived when its fecundity was high (upper left quarter). On the right side of the graph, species 2 had a higher growth rate than species 1 and the pattern was reversed. Both the upper left and lower right quarters of the figure corresponded to cases of classical

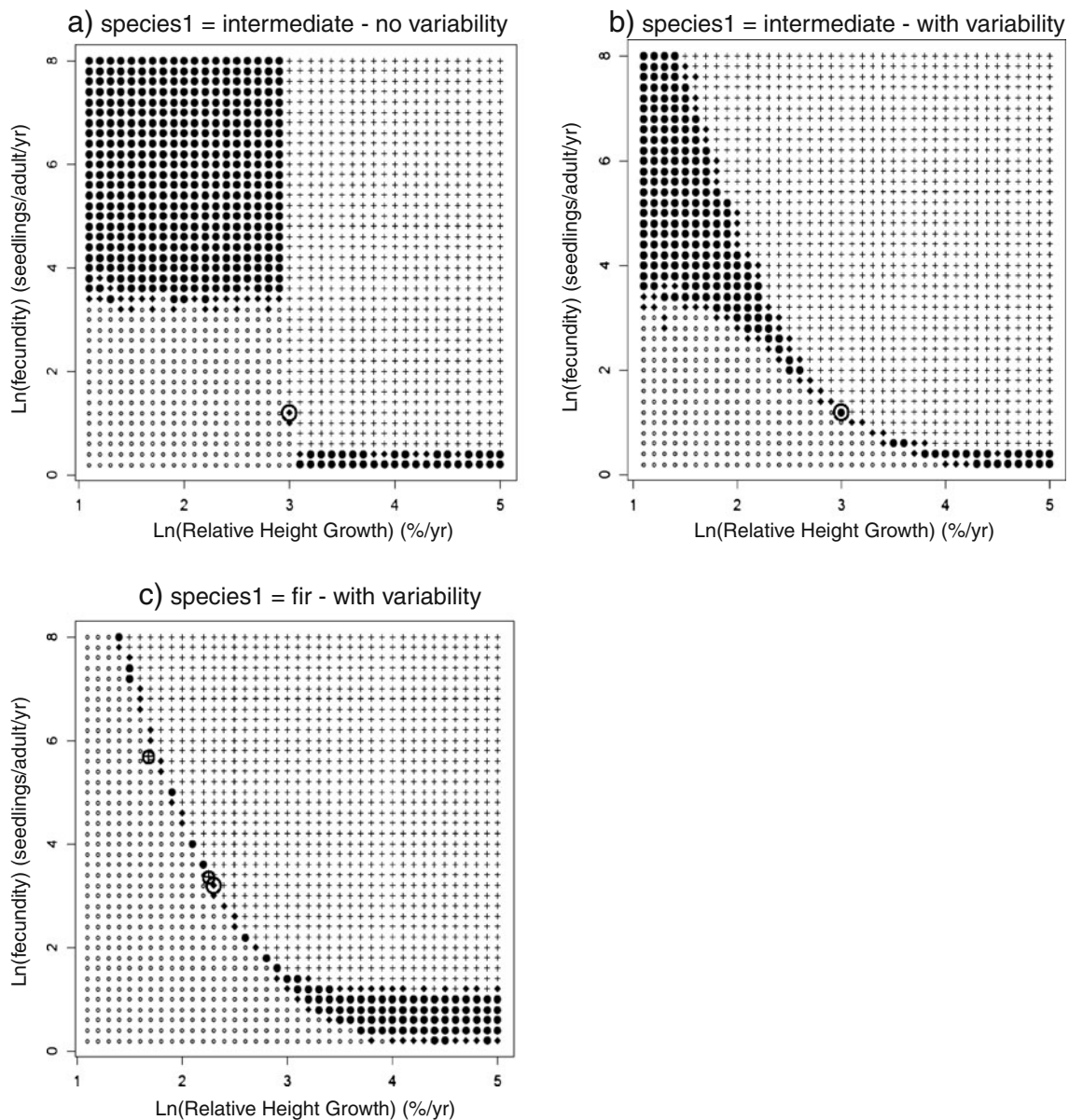


Fig. 1 Patterns of coexistence in the parameter space of species 2. The location of species 1 in the parameter space of species 2 is represented by a circled dot. Each symbol represents the result of five simulations with different initial relative abundances: (1) *Cross* exclusion of species 1; (2) *white dot* exclusion of species 2; (3) *black dot* coexistence of both species at the end of the simulation; (4) *black diamond* undetermined result (variable between simulations). **a** Species 1 of intermediate fecundity and growth, no intra-specific variability (first experiment). Coexistence is possible in three contrasted situations (black dots): species 2 is an inferior competitor with superior fecundity (higher left quarter), species 2 is a superior competitor with inferior fecundity (lower right quarter), species 2 and

niche coexistence between a seed-limited superior competitor and a fugitive highly fecund inferior competitor. The graph shows that both species coexisted also at the end of the simulation when species 2 had exactly the same parameters as species 1. This case corresponded to unstable

species 1 have the same parameters (circled black dot). **b** Species 1 of intermediate fecundity and mean growth, with intra-specific variability for both species (second experiment). The coexistence region (black dots) is continuous. Coexistence requires that species 2's life traits remain within inferior and superior boundaries, indicating a necessary trade-off. **c** Species 1 corresponding to European fir, with intra-specific variability for both species (third experiment). Norway spruce and European beech are represented by crossed circles. Because of high European fir fecundity, the coexistence region is restricted to a narrow band on the left side of the graph. Norway spruce and European beech appear close to meeting the conditions of coexistence with European fir

coexistence. Unstable and stable coexistence appeared apart on the graph, indicating a discontinuity of processes between these two types of coexistence.

In the second experiment, adding intra-specific variability profoundly modified the coexistence patterns (Fig. 1b).

A decrease in the distance between species along the mean growth axis corresponded to an increase in seedling growth distribution overlap. The separation between coexistence regions disappeared and they became a single region narrowing at the point of unstable coexistence, where overlap was complete. On the left side of the graph, where the mean growth of species 2 was lower than the mean growth of species 1, coexistence was possible only if the fecundity of species 2 was between a lower and an upper limit. Indeed when species 2 was more fecund than the upper limit, it was able to exclude species 1, despite lower mean growth. A symmetric situation occurred on the right side of the graph. Continuity appeared between stable and unstable coexistence. Coexistence was possible between species that were only slightly different provided that the proper trade-off between fecundity and mean growth was respected. When species differed more, a trade-off was still necessary for coexistence but the required tuning was less precise. Some exclusion cases in experiment 1 (no intra-specific variability) became coexistence cases in experiment 2 (intra-specific variability added), but the reverse was also true. Globally, intra-specific variability did not increase coexistence systematically.

Figure 1c represents the pattern of coexistence obtained when species 1 had parameters corresponding to European fir. Because of its high fecundity, possibilities of coexistence with a species 2 of lower mean growth and higher fecundity were restricted to a very narrow area on the left side of the graph. Greater possibilities of coexistence appeared on the right side of the graph, with a species 2 of lower fecundity and a higher mean growth rate. Plotting Norway spruce and European beech on the graph indicated that both these species were excluded by European fir either when spruce–fir or beech–fir stands were simulated. Nevertheless, these species appeared to be very close to meeting the conditions necessary for coexistence with fir.

Patterns of abundances, exclusion time and equilibrium stability

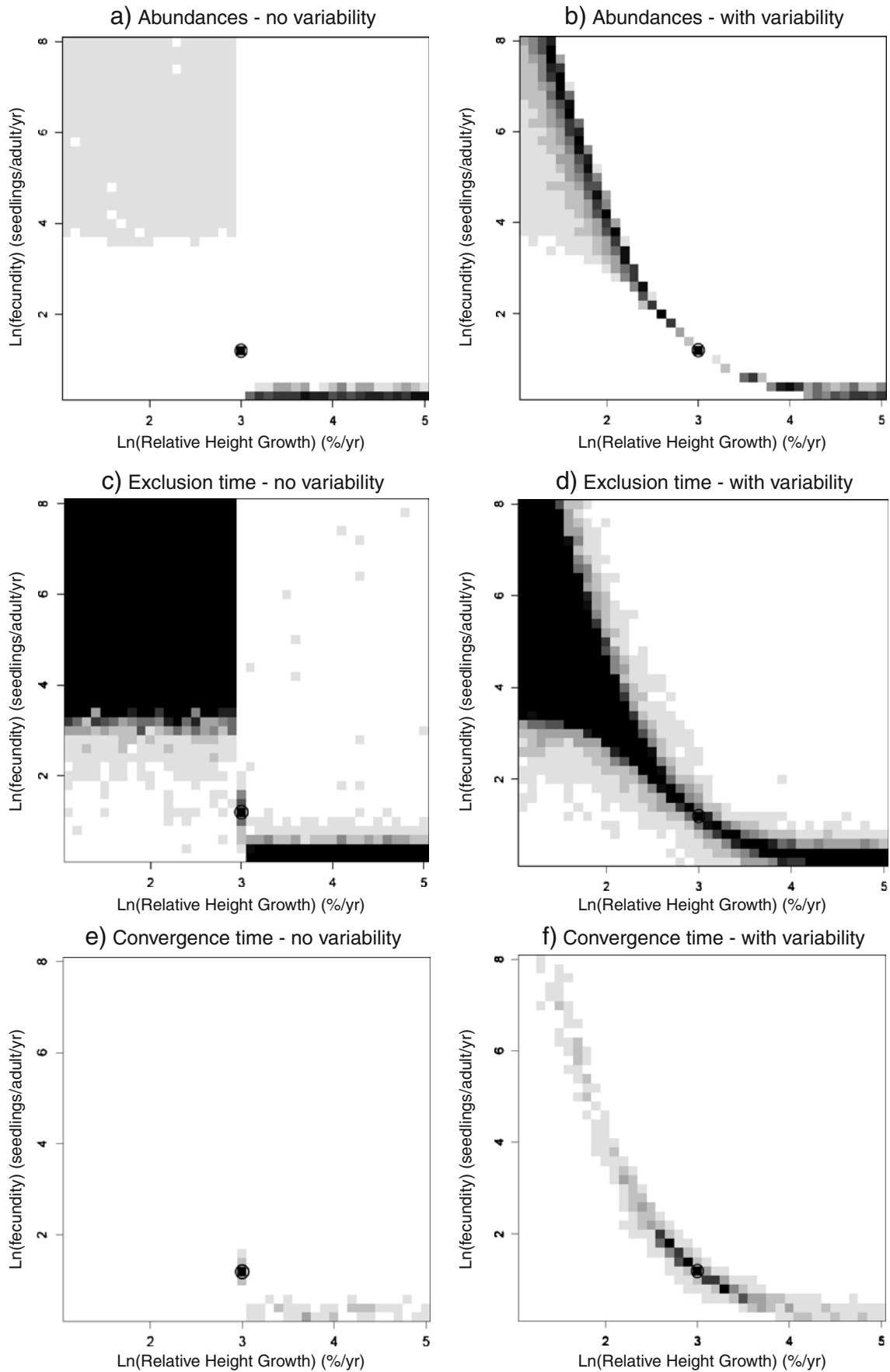
Without intra-specific variability, the abundance of the superior competitor did not depend on the parameters of the inferior competitor (Fig. 2a). When species 2 had a lower mean growth rate and higher fecundity than species 1, respective abundances did not vary much with the location of species 2 in the region of coexistence (upper left corner). In these cases, the abundance of species 1 did not depend on species 2, and the abundance of species 2 was constrained by the availability of patches left over by species 1. When species 2 had a higher mean growth rate and lower fecundity than species 1 (lower right corner), its abundance at equilibrium varied only in correlation to its own fecundity and species 1 occupied the remaining

patches. When both species had same parameters, they reached the same abundance at the end of the simulation (50% abundance for the rarest species) but this coexistence is unstable.

In contrast, the abundance of both species varied regularly when intra-specific variability was included (Fig. 2b). A concave out axis of equal abundances crossed the parameter space, indicating the trade-off relation between species 2's mean growth and fecundity leading to the same level of performance as species 1. When species 2 was more distant from species 1 along this axis of equal abundances, its performance remained the same, despite a change in competition–colonisation strategy. When species 2's distance from this axis increased in the upward right direction (towards higher mean growth and fecundity), its performance and abundance increased up to the boundary of the area of coexistence where it eliminated species 1. When species 2's distance from the axis increased in the downward left direction (towards lower mean growth and fecundity), its performance decreased, reaching extinction. When both species were fecund (upper left corner), the area of coexistence was relatively wide, allowing for a smooth gradient of abundances.

Without intra-specific variability, the map of exclusion time (Fig. 2c) showed an abrupt separation along the vertical line of competitive hierarchy reversal. In each section of this graph, exclusion time increased with the

Fig. 2 Patterns of equilibrium abundances, exclusion time and convergence time. Species 1 of intermediate fecundity and mean growth, with or without intra-specific variability for both species (second experiment). **a, b** Equilibrium abundances. Colours represent the levels of abundance at equilibrium of the rarest species, from *black* (abundance between 0% and 5%) to *white* (abundance between 45% and 50%). A pivotal trade-off axis corresponds to cases where the abundance of the rarest species is close to 50% (both species have about the same abundances). **a** No intra-specific variability: In the upper left corner, species' relative abundances is determined only by the parameters of species 1 (the reference species) and does not depend on the parameters of species 2. **b** with intra-specific variability: Species 1 is the rarest species above the line of equal abundances, while species 2 is the rarest below the line. **c, d** Exclusion time. Colours represent exclusion time from *black* (exclusion before 50 iterations) to *white* (no exclusion before the end of the simulation at 500 iterations). **c** No intra-specific variability: A dramatic shift separates coexistence and exclusion depending on species 2's mean growth. **d** With intra-specific variability: Exclusion time decreases with the distance from the coexistence region boundary. **e, f** Convergence time. Colours represent the time needed for simulations starting from five different initial conditions to converge to equilibrium abundances. **e** No intra-specific variability: Convergence is very fast in most cases, either to stable equilibrium or to exclusion. The case where both species have the same parameters appears as a notable exception. **f** with intra-specific variability: Convergence time changes along two complementary directions: it increases as species 2 approaches the trade-off axis of equal species equilibrium abundances, and it increases along this axis with species similarity. Along the ideal coexistence trade-off axis, equilibrium stability decreases with species similarity



difference of fecundities between species but did not depend on the exact values of mean growth rates. In contrast, when intra-specific variability was included (Fig. 2d), exclusion time decreased smoothly with the distance from the border of the coexistence region, in relation to fecundity and mean growth rate of species 2, both when it had a higher and a lower mean growth rate than species 1.

Without intra-specific variability, a short convergence time indicated high equilibrium stability for almost every situation (Fig. 2e). Either one species was excluded rapidly or both species converged rapidly to positive equilibrium abundances, independently of initial abundances. The case of similar parameters for both species appeared as an exception as it showed no sign of convergence. A detailed simulation analysis indicated that in that case, an initially rare species remained rare and was susceptible to random extinction, a feature of unstable coexistence. Despite stable coexistence, convergence was relatively slow when species 2 was the superior competitor but had very low fecundity (lower right corner) because the rise in its population was limited by small colonisation ability.

With intra-specific variability (Fig. 2f), convergence time varied regularly, indicating a gradient of equilibrium stability depending on species differences both in fecundity and mean growth rate. Stability increased with the distance between species along the axis of equal abundances, as the strategy of species 2 became more dissimilar from the strategy of species 1 despite the same level of performance. It also increased with the distance on each side of the axis towards the border of the area of coexistence. When both species were fecund (upper left corner), coexistence stability appeared high despite substantial differences in species abundances at equilibrium.

Discussion

Intra-specific variability shifts trade-off conditions of species coexistence

In this study, intra-specific variability shifted the conditions of trade-off necessary for coexistence. This result contrasts with previous approaches focussing only on cases where intra-specific variability was described as beneficial to coexistence (Begon and Wall 1987; Clark 2010; Clark et al. 2007) or suggesting a limited effect (Lichstein et al. 2007). In the present study, it promoted coexistence when it prevented the exclusion of a relatively fecund species by increasing the competitive ability of its best seedlings, but penalised coexistence when it made this fecund species able to exclude its competitor. In both cases, intra-specific variability disproportionately favoured the more fecund

species because the higher tail of the distribution represented more individuals when fecundity was high.

By allowing species performance to overlap, the effect of intra-specific variability was to reduce inter-specific competition asymmetry. The resulting effect was in agreement with weighted lottery models where competition asymmetry is regulated by a parameter. Kisdi and Geritz (2003), observed thus that relaxing competition asymmetry shifted the conditions of coexistence towards higher fecundity requirements for the best competitor. Calcagno et al. (2006) also observed that beyond a level of fecundity differences, the better colonist could exclude the better competitor and destroy coexistence. Our work shows how such imperfect competition asymmetry could be related to intra-specific life trait variability.

Intra-specific variability did not systematically increase the balance between species abundances at equilibrium but produced a whole gradient of relative abundances. Traditional competition–colonisation patch models where competition is fully asymmetric have led to the idea that the abundance of a superior competitor may be not influenced by the presence of an inferior competitor (Hastings 1980; Levins and Culver 1971; Tilman 1994); this is what we obtained without intra-specific variability. In contrast, with intra-specific variability, all levels of abundances were possible for both species, depending on their interactions.

Intra-specific variability allows a gradient between stable and unstable coexistence

Instead of a sharp contrast between situations of exclusion or coexistence, intra-specific variability allowed a smooth transition between exclusion, unstable coexistence and stable coexistence. In a seminal article, Chesson (2000b) associated stable coexistence to niche processes and unstable coexistence to neutral processes; and proposed a continuum of equilibrium stability between these extremes.

In our simulations without intra-specific variability, unstable coexistence appeared to be an isolated situation, limited to the case where both species had the same parameters. Small differences in life traits immediately destroyed coexistence. This effect, already noted by other authors (Zhang and Lin 1997; Zhou and Zhang 2008), has been an argument against the idea that species traits can be “neutral”. Without intra-specific variability, other cases of coexistence were set apart from the case of similar parameters for both species by the fact that stable coexistence required high differences of species fecundities. In contrast, when intra-specific variability was simulated, our graph of coexistence showed a continuum between unstable and stable coexistence. Along the axis of equal equilibrium abundances, coexistence was unstable when both species had the same parameters and stability increased progressively

with species dissimilarity, giving a graphical support to Chesson's proposition (Chesson 2000b).

In classical asymmetric competition–colonisation models, the difference between species colonisation rates required for stable coexistence has often been interpreted as a limit to similarity between coexisting species (Kinzig et al. 1999). More recently, Calcagno et al. (2006) have interpreted a destruction of coexistence when the difference between fecundities is too high as a limit to dissimilarity. Nevertheless, in both cases, relative species performance varied with fecundities. The observed limits were more simply an expression of the range of competition–colonisation trade-off allowing coexistence. In contrast, species similarity must be discussed for a given level of relative performance (Levine et al. 2008). Along our axis of equal equilibrium abundance, species performance remained the same despite a shift of strategy. Neither limit to similarity nor limit to dissimilarity appeared along this axis, in line with previous studies that showed that despite its popularity, the concept of limiting similarity has been supported by few models and is difficult to demonstrate in the field (Abrams 1983; Chesson 2000a).

Following Chesson, Adler et al. (2007) proposed that coexistence could reflect either strong stabilising mechanisms overcoming large fitness differences or weak stabilisation operating on species with similar fitness. In our case, the area of coexistence widened when differentiation increased. This can be interpreted as if high stabilisation through differentiation allowed large variations in strategies of coexisting species and high variations in performance, reflected by variations in relative abundances. In contrast, around the point where both species had the same parameters, the area of coexistence narrowed and unstable coexistence required high strategy similarity.

Another group of authors has proposed to unify niche and neutral theories by adding stochasticity in models where species had overlapping environmental niches (Gravel et al. 2006; Scheffer and van Nes 2006; Tilman 2004). In these models, coexistence relied on environment heterogeneity that directed species spatial distribution. Stochasticity reduced niche partitioning between species, making coexistence less stable. The complementary case we addressed corresponded to spatially homogeneous competitive environments (Amarasekare 2003, 2004). In our context, intra-specific variability could either reduce or increase species difference of performances. As a result, it did not systematically decrease stability.

Intra-specific variability may have a huge influence on natural communities by influencing simple niche differentiation mechanisms

We showed in this work that intra-specific variations could play a key role in community dynamics by modulating

simple niche differentiation mechanisms. Our reference to Norway spruce, European fir and European beech was limited by the fact that the model collapsed juvenile development in only one phase. Field data allowed here nevertheless give a practical sense to the model and approach realistic parameter orders of magnitude.

Intra-specific variability is usually discarded as noise in models and experimental approaches (Clark et al. 2004, 2007) but when quantified, it is usually high, both in plant ({Albert, #1685}{Chave 2004 #1069}) and animal communities (Mason et al. 2008). This is particularly true for traits related to size and growth performance, that determine resource partitioning and optimal foraging (Tokeshi 1999). We focussed this work on variability in juvenile growth because it can regulate competition asymmetry. Intra-specific variability in adult mortality is more difficult to relate to field data because mortality occurs only once per individual. Probabilities of mortality can then be evaluated in practice only on sub-populations but not really at the individual level. We did not test either the potential effect of intra-specific variability in individual fecundities because as dispersion was random in the model, differences in individual fecundities would not have translated into differences of local seedling densities or local seedling traits. Nevertheless, this would not be the case with a model of local dispersion and/or heritability and these processes constitute interesting development perspectives. Another axis of development consists in taking into account environmental covariables and covariance between individual responses (Clark et al. 2007). Relations between parameters at the individual level can indeed reveal subtle niche differences among species (Clark 2010; Clark et al. 2010).

Experimental work and field observations could be designed to test the influence of intra-specific variability on competition and community dynamics. Experimental work is being done at the moment to study the effect of species similarity on coexistence stability (Cadotte 2007; Levine et al. 2008). Complementary experiments explicitly manipulating the distribution of traits within populations could be developed. If a substantial influence of intra-specific variability was confirmed, this would mean that intra-specific functional variability should be evaluated in the field in addition to classical comparisons of species' mean traits {Albert et al. 2010 #1685} and integrated into community dynamic models (Clark 2007). Intra-specific variability could indeed provide a key to subtle variations in community dynamics and structure.

Individual effects and phenotypic variations in space and time

In this work, we drew individual effects in distributions that did not change between generations or with individual

spatial locations. This approach is a simplification of the spatio-temporal structure of phenotypic variation, which combines genetics and plastic responses to the environment. Genetic variation is heritable across time and selection occurring on parents determines genes availability at the next generation. The distribution of individual effects should change with time to take this effect into account. In this context it would be very interesting to test for convergence versus differentiation among species. In the case of plasticity, plants vary their phenotype in response to environmental conditions which depend on spatial location. The distribution of individual effects should then change with space. This could potentially lead to local competition relations unpredictable at the scale of the community {Clark 2010 #1675}. Going further into a detailed analysis of the effects of intra-specific variability appears essential to long term predictions in community dynamics (Herauld 2007; Scheffer and van Nes 2006; Vellend 2006; Vellend and Geber 2005).

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