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Forest fragmentation shapes the alpha-gamma relationship in plant diversity

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Accepted Article

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ABSTRACT

Questions: Forest fragmentation affects biodiversity locally (α-diversity) and beyond – at relatively larger scales (γ-diversity) – by increasing dispersal and recruitment limitations. Yet, does an increase in fragmentation affects the relationship between α- and γ-diversity and what can we learn from it?

Location: Northern France.

Methods: We surveyed 116 forest patches across three fragmentation levels: none (continuous forest); intermediate (forest patches connected by hedgerows); and high (isolated forest patches). Plant species richness of both forest specialists and generalists was surveyed at five nested spatial resolutions across each forest patch: $1m^2$; $10m^2$; $100m^2$; $1000m^2$; and total forest patch area. First, we ran log-ratio models to quantify the α ~ γ relationship. We did that separately for all possible combinations of fragmentation level (none *vs*. intermediate *vs*. high) × spatial scale (e.g. α-$1m^2$ *vs*. γ-$10m^2$) × species type (e.g. α-specialists *vs*. γ-specialists). We then used linear mixed-effects models to analyze the effect of fragmentation level, spatial scale, species type and all two-way interaction terms on the slope coefficient extracted from all log-ratio models.

Results: We found an interaction effect between fragmentation level and species type, such that forest specialists shifted from a linear (i.e. proportional sampling) to a curvilinear-plateau (i.e. community saturation) relationship at low and high fragmentation, respectively, while generalists shifted from a curvilinear to a linear pattern.

Conclusions: The impact of forest fragmentation on the α ~ γ relationship supports generalist species persistence over forest specialists, with contrasted mechanisms for these two guilds. As fragmentation increases, forest specialists shift from proportional sampling towards community saturation, thus reducing α-diversity likely due to dispersal limitation. *Per contra*, generalists shift from community saturation towards proportional sampling, thus increasing α-diversity likely due to an increase in the edge:core ratio. To ensure long-term conservation of forest specialists, single large should be preferred over several small forest patches.

KEYWORDS

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Community assembly, anthropogenic disturbances, alpha diversity, gamma diversity, dispersal limitations, habitat fragmentation, local-regional richness relationship, metacommunity dynamics, habitat conservation strategies

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INTRODUCTION

Habitat loss and fragmentation (i.e. the breakdown of large and contiguous habitats into smaller and more isolated patches) is widely acknowledged as a major cause of biodiversity loss (Wilcox & Murphy 1985; Tilman 2004). Many empirical and theoretical studies have investigated the effects of habitat loss and fragmentation on species richness at different spatial scales from local (i.e. α-diversity) to large (i.e. γ-diversity) scale (Riitters et al. 2000; Fahrig 2013; Rybicki & Hanski 2013; Carrara et al. 2015; Hanski 2015; Valdés et al. 2015; Baynes et al. 2016). A decrease in habitat patch size results in lower species richness due to both direct and stochastic area-dependent extinction (Pimm et al. 1988; Few et al. 2004). Increased habitat patch isolation magnifies dispersal limitations, thereby impeding metacommunity processes (e.g. rescue and mass effects; Leibold et al., 2004) and ultimately reducing regional species richness first (Cornell & Lawton, 1992) before reducing local species richness of all habitat patches (Jamoneau, Chabrerie, Closset-Kopp, & Decocq, 2012). Moreover, the increase in the edge:core ratio following fragmentation alters habitat quality, which has been shown to be particularly detrimental to habitat specialists (Mortelliti et al. 2011). *Per contra*, generalist species already inhabiting the habitat patches or originating from the surrounding landscape may benefit from an increase in the edge:core ratio, thereby altering species richness within the habitat patches (Vandermeer & Carvajal 2001; Hanski 2015). Habitat fragmentation *per se* (i.e. the breaking apart of habitat after controlling for habitat loss) (Fahrig 2003) and management of the landscape matrix may thus alter the relationship between α- and γ-diversity (*sensu* Belote, Sanders, & Jones, 2009; Cornell & Lawton, 1992; Starzomski, Parker, & Srivastava, 2008). But surprisingly, how fragmentation impacts this α ~ γ relationship – and potentially decouples α- and γ-diversity – has received little attention so far.

Local species assemblages result from the interaction between local processes (e.g. competition, disturbance) and processes operating at broad scales (e.g. dispersal) (Ricklefs 1987). The relative importance of these two processes and the spatial scale at which they operate are commonly investigated by regressing α- against γ-diversity (Harrison & Cornell, 2008; He, Gaston, Connor, & Srivastava, 2005; Hillebrand & Blenckner, 2002; Leibold et al., 2004), hereafter referred as the α ~ γ relationship (AGR). A positive linear relationship indicates that the local community proportionally samples the set of species available at a larger spatial extent (i.e. the number of species present in a larger area determines the local community: α- and γ-diversity

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are coupled), whilst a curvilinear-plateau relationship reflects community saturation (i.e. local species interactions limit the number of species that can locally coexist: α- and γ-diversity are decoupled) (Cornell & Lawton, 1992; Srivastava et al., 2008). However, these patterns have been shown to depend upon environmental severity/stress, with community saturation being predominant under both benign and severe environmental conditions, while proportional sampling dominates under intermediate positions along the environmental severity gradient (Michalet et al., 2015). Since fragmentation can be considered an edge-initiated disturbance impacting environmental conditions, we might expect a similar influence of fragmentation on the AGR. Moreover, the AGR may also change in the course of forest succession, with pseudo-saturation (*sensu* Lawton & Strong (1981)) in early stages due to the quick colonization of good dispersers, unsaturation at intermediate stages and saturation in late-successional stages following competitive exclusion (Srivastava et al. 2008).

Forest patchiness is not only the result of fragmentation *per se*, but also the result of the afforestation of former agricultural lands at different times (Herault & Honnay 2005). Forest fragmentation may thus not only happen under habitat loss conditions, but also under stable forest cover conditions and even under forest gain (Estreguil et al. 2013). This means that total species richness may even increase as fragmentation increases until the level of fragmentation reaches a threshold that is detrimental to biodiversity as a whole such that total species richness in the landscape decreases. To illustrate this, consider a set of plant communities connected to each other's within a continuous forest matrix (Fig. 1, left panel). Here, forest specialists (FS), i.e. species that are more or less restricted to closed-canopy forest as habitat (Carrara et al. 2015; Valdés et al. 2015; Schlinkert et al. 2016), dominate plant communities. Now, consider a set of plant communities within a fragmented forest surrounded by grasslands but still connected to each other's by linear woody elements (e.g. hedgerows) (Fig. 1, central panel). Then, forest generalists (FG), i.e. species that prefer forest edges and clearings but may survive closed forest conditions (Valdés et al. 2015), are likely to enter the forest patches and co-occur with forest specialists, thereby increasing the number of species co-occurring within the same forest patches compared with the situation in the non-fragmented forests. Finally, if we disconnect forest patches and intensify agricultural practices in the surrounding landscape (Fig. 1, right panel), we expect a negative effect primarily on forest specialists, and ultimately on generalists, by boosting extinction

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cascades and by limiting immigration (Fischer & Lindenmayer, 2007) so that the total number of species will drop.

The pure effect of fragmentation on the AGR will depend upon the balance between colonization and extirpation events that happen at both the local community scale and the larger forest patch scale. Colonization events of a new plant species not yet occurring within a given forest patch will first happen at the scale of the forest patch before it can happen at the local scale of a given plant community inside the forest patch. *Per contra*, extirpation events of a given plant species will occur faster at the local community scale than at the entire forest patch scale reflected as richness loss at the α-diversity level first, before it can translate to the γ-diversity level. These processes are predicted to be more pronounced in small forest patches and/or within intensively managed agricultural landscapes because of stronger edge effects (e.g. increased light and nutrient levels) which favor generalist plant species at the expense of forest plant specialists (Bossuyt, Heyn, & Hermy, 2000; Michalet et al., 2015; He et al., 2005). Based on these considerations, we propose separate research hypotheses for forest specialists and generalists regarding the impact of forest fragmentation on the AGR (Fig. 1). As the level of fragmentation increases, we hypothesize a shift from proportional sampling and stochastic selection (i.e. α-diversity is coupled to γ-diversity and increases linearly as γ-diversity increases) to more deterministic community saturation due to competition (i.e. α-diversity is decoupled from γ-diversity and reaches a threshold as γ-diversity increases) for forest specialists (see before last row in Fig. 1) while the opposite pattern is expected for generalists (see last row in Fig. 1). In addition to this interaction effect between the fragmentation level and species type, we also assume different shapes of AGR for specialists and generalists depending on the difference in spatial resolution between α- and γ-diversity, with community saturation more likely to occur when this difference is large (Loreau 2000). To test these research hypotheses, we used the most recent scientific advances to assess the AGR (Szava-Kovats, Ronk, & Pärtel 2013) of both forest specialists and generalists at several spatial resolutions and across several landscapes in northern France (Hauts-de-France), differing in the level of forest fragmentation, i.e. from non- (fake patches within a forest matrix), to semi- (small, connected patches within a matrix of grasslands) and highly-fragmented (small, isolated patches within a matrix of crop fields) systems. Results from this study will have important implications for landscape planning and biodiversity conservation, notably to preserve forest specialist species which are also the most threatened species in a context of forest fragmentation and management intensification of agricultural landscapes.

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MATERIALS AND METHODS

Study area

The study area is located in northern France (N49°25'–50°11'; E1°52'–3°55'; alt. from 60 to 220 m) (Fig. 2). The climate is oceanic with a mean annual temperature of 10°C and total annual rainfall of 700 mm. The geological substrate is dominated by Cretaceous chalks, usually covered by Quaternary loess. The study region is dominated by croplands, intensively cultivated for cereals, rapeseed and sugar beet.

Study design and vegetation survey

We selected three replicates of 5 km × 5 km landscape windows for each of the three studied types of landscape covering a contrasted gradient of forest fragmentation from non-fragmented forests (NF) to "openfield" landscapes or highly-fragmented forests (HF) throughout "bocage" landscapes or semi-fragmented forests (SF). The three SF windows consist in small forest patches embedded in a grassland-dominated matrix and connected by hedgerow while the three HF windows consist of small, isolated forest patches surrounded by intensively cultivated croplands. In each of these six landscape windows, we randomly selected 15 forest patches with sizes and shapes allowing us to set up a 1000 m^2 quadrat at the center of the forest patch so that the closest forest edge was located at a minimum distance of 10 m. Whenever a window had less than 15 forest patches meeting these criteria, several non-overlapping quadrats (two to four) were arranged within the same large forest patch. For the three NF windows, we created virtual forest patches that mimicked the number, size and shape of the true forest patches found in the six other landscape windows (see Jamoneau, Chabrerie, Closset-Kopp, & Decocq, (2012) for more details on how virtual forest patches were delineated in the landscape). A total of 135 quadrats (9 windows × 15 quadrats) were installed across 116 forest patches, including 39, 36 and 41 forest patches in NF, SF and HF systems, respectively (see raw data in Appendix S1). Note that some landscape windows had less than 15 forest patches of sufficient size (1000 m^2). In this case, we used the largest forest patches available within the focal landscape window to set up several quadrats of 1000 m^2 within the same forest patch. Yet, because it happened only little (ca. 10% of the case), we did not account for this limited pseudo-replication issue of having at most 4 quadrats of 1000 m^2 each (this case happened only once) belonging to the same very large patch (> 100 ha).

Between 2007 and 2008, all 116 forest patches were visited twice, in spring (April–May) and in summer (June–September): we walked along parallel transects located 10 m apart from

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each other to record all vascular plant species. We thus obtained a value of species richness per forest patch, i.e. patch-scale diversity. In addition to patch-scale diversity, specific floristic surveys were carried out at four nested spatial resolutions within each of the 135 quadrats of 1000 m^2, using a logarithmic nested-plot design (see Fig. 1c in (Wasof et al. 2018)): 1 m^2; 10 m^2; 100 m^2; and 1000 m^2.

We focused on vascular plant species occurring within the herbaceous layer (height < 1 m) solely as it better reflects spontaneous vegetation than in the shrub (height from 1 to 8 m) and tree (height > 8 m) layers which are more dependent on forest management practices. Note, however, that tall individuals of herb, fern, sedge or grass species which height exceeded the 1-m limit of the herbaceous layer were counted as part of the herbaceous layer. Intraspecific taxa (e.g. subspecies *picra* and *pratensi*s of *Cardamine pratensis*) and taxonomic agglomerates (e.g. *Rubus fruticosus* agg., *Taraxacum officinale* agg.) were treated as single species. Finally, each of the 175 herbaceous plant species recorded across our study area was classified as either a forest specialist (FS: n = 43) or a forest generalist (FG: n = 132) (Appendix S2) (Oberdorfer 1957).

Patch characteristics, habitat quality and the proportion of forest within the landscape

To correct for the effects of patch characteristics (area, length and age), habitat quality (soil and light conditions) and the amount of habitat around the focal forest patch (proportion of forest habitat within the landscape) on the AGR, we prepared several variables (Appendix S3) to be included as covariates in all the log-ratio models we ran (see next subsection entitled "Data analysis"). Including these covariates in the log-ratio models allowed us to determine the shape of the AGR for different levels of fragmentation, scale and species type, but independently from potential confounding effects due to differences in patch size, patch age, patch quality and forest loss or gain in the surrounding landscape (here we are interested in the pure effect of habitat fragmentation and not in habitat loss or gain which may confound with habitat fragmentation *per se*).

Data analysis

To assess the shape of the AGR, we not only considered FS and FG separately but we also considered the total diversity (FS+FG), thus leading to three possible relationships among species types that we tested: (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$; (2) $\alpha_{FS} \sim \gamma_{FS}$; and (3) $\alpha_{FG} \sim \gamma_{FG}$. Hence, we assessed the shape of the AGR for all possible combinations of species type relationship ($\alpha_{FS} \sim \gamma_{FS}$, $\alpha_{FG} \sim \gamma_{FG}$,

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$\alpha_{FS+FG} \sim \gamma_{FS+FG}$) × fragmentation level (NF, SF, HF) × spatial scale (e.g. α-1m^2 *vs*. γ-10m^2), while controlling for the effect of several covariates (Appendix S3). Like in Belote et al. (2009), we considered species richness of any spatial resolution nested within a larger one as α-diversity relative to the species richness in the larger plot which we considered as γ-diversity. This leads to a total of ten combinations of nested spatial scales: (1) α-1m^2 *vs*. γ-10m^2; (2) α-1m^2 *vs*. γ-100m^2; (3) α-1m^2 *vs*. γ-1000m^2; (4) α-1m^2 *vs*. γ-total; (5) α-10m^2 *vs*. γ-100m^2; (6) α-10m^2 *vs*. γ-1000m^2; (7) α-10m^2 *vs*. γ-total; (8) α-100m^2 *vs*. γ-1000m^2; (9) α-100m^2 *vs*. γ-total; and (10) α-1000m^2 *vs*. γ-total.

To assess the shape of the AGR, we ran a multiple-regression version (Equation 1) (see Appendix S4 for more details) of the log-ratio model proposed by Szava-Kovats, Zobel, & Pärtel (2012) for each landscape window separately, for a given nested spatial scale combination (e.g. α-1m^2 *vs*. γ-10m^2) and for a given combination of species type relationship (e.g. $\alpha_{FS} \sim \gamma_{FS}$). This makes a total of 270 log-ratio models: three fragmentation levels × three replicates per fragmentation level × ten nested spatial scales × three species type relationships. For each of these 270 possible combinations, we ran a linear regression with log(α/(γ-α)) as the response variable and log(γ) as the main predictor variable while accounting for several covariates: patch *area*, *length* and *age*; soil *pH*, *C:N* and *P*; *light* conditions (SCA); and the proportion of forest within a 500-m radius (*for500*) (see Appendix S3 for more information on the covariates). All covariates were standardized prior to analysis, i.e. the value for each variable was subtracted from its mean and divided by its standard deviation (Schielzeth 2010).

$$\ln\left(\frac{\alpha}{\gamma-\alpha}\right) \sim \ln(\gamma) + area + length + age + pH + C{:}N + P + light + for_{500}$$

Equation 1

Once the 270 log-ratio models were fitted, we extracted the slope coefficient of log(γ), which provides a quantitative estimate of the shape of the AGR. Then, we split the 270 slope coefficients into two different datasets: (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90) and (2) $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ (n = 180). For both datasets, we built several candidate models (i.e. step 2 in our analyses) to explain the observed variation in the *slope* coefficient (i.e. the response variable). As explanatory variables, we tested the effect of fragmentation level (*frag*: NF, SF, HF), spatial scale (*scale*: 1, 2, 3, 4), species type (*sp*: FS *vs*. FG) as well as all possible two-way interactions between all three

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variables. More specifically, we tested nine candidate models: (1) *slope ~ frag + sp*; (2) *slope ~ frag + scale*; (3) *slope ~ frag × sp*; (4) *slope ~ frag × scale*; (5) *slope ~ frag + scale + sp*; (6) *slope ~ frag × sp + scale*; (7) *slope ~ frag × scale + sp*; (8) *slope ~ frag + scale × sp, and* (9) *slope ~ frag × scale × sp*. Spatial scale was here treated as a semi-quantitative (ordinal) variable measuring the nestedness factor between α- and γ-diversity (e.g. α-1m^2 *vs*. γ-10m^2, α-1m^2 *vs*. γ-100m^2, α-1m^2 *vs*. γ-1000m^2 and α-1m^2 *vs*. total patch area have nestedness factor of 1, 2, 3 and 4, respectively). Note that for the first dataset ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$), which focuses on all herbaceous plants without distinguishing between specialists and generalists, we could only test the effect of fragmentation level, spatial scale and the interaction between the two, thus leading to two candidate models only (*slope ~ frag + scale vs*. *slope ~ frag × scale*). To run our candidate models with the slope of the log-ratio models as the response variable, we used a linear mixed-effects modelling (LMM) approach with the three replicates per fragmentation level as well as the ten combinations of nested spatial resolutions as random intercept terms. To compare candidate models with nested fixed effects (but with the same random structure), we used maximum likelihood (ML) estimation instead of restricted maximum likelihood (REML) (Zuur et al. 2009). As the best candidate model, we selected the model with the smallest Akaike information criteria (AIC) and rerun the selected best model using REML for final inference and reporting of the models' parameters (Zuur et al. 2009).

All statistical analyses were performed using the "lme4" (Bates et al. 2015), "nlme" (Pinheiro, 2002), "broom" (Robinson 2014), "MuMIn" (Grueber et al. 2011), "glmm" (Green & MacLeod 2016), "mvtnorm" (Genz & Bretz 2009), "digest" (Genz & Bretz 2009) and "Matrix" (Fiske & Chandler 2011) packages in the R software environment version 3.4.1 (R Core Team 2017).

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RESULTS

In general, we found that the slope parameter of the $\alpha \sim \gamma$ relationship (AGR) of herbaceous forest plants is close to zero (mean ± standard deviation: -0.281 ± 0.85; n = 270) and does not significantly differ from zero (p-value = 0.1185, see Appendix S5 for detailed 'one sample t-test' for the distribution of the 270 slope values & detailed 'Anova' outputs for all the studied candidate models), suggesting linear patterns (Type I) to predominate (see Appendix S6). Focusing on the log-ratio models relating α to γ diversity of all forest species, combining forest specialists with generalists ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$) (-0.11 ± 0.22) (n = 90) (Fig. 3a), the best model (*slope* ~ *frag* + *scale*) showed a significant effect of fragmentation but no effect of spatial scale on the shape of the AGR (Table 1, see Appendix S7 for the output of other candidate models). Accordingly, the AGR shifted from a linear (Type I) to a curvilinear (Type II) pattern as the level of fragmentation increased (Fig. 3a and Fig. 4a). For the log-ratio models relating α to γ diversity of either forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) (-0.574 ± 1.06) (n = 90) (Fig. 3b) or generalists ($\alpha_{FG} \sim \gamma_{FG}$) (-0.188 ± 0.789) (n = 90) (Fig. 3c), we found a significant interaction effect between fragmentation and species type but no effect of spatial scale (best model: *slope* ~ *frag* × *sp*) (Table 1, see Appendix S7 for the output of other candidate models). The AGR of forest specialists showed a shift from Type I to Type II curves as the fragmentation level increased from non-fragmented to highly-fragmented systems, while the AGR of forest generalists showed the complete opposite pattern; shifting from Type II to Type I as the fragmentation level increased (Appendix S6 and Figs. 4b and 4c).

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DISCUSSION

Even after accounting for forest patch characteristics, habitat quality and the proportion of forest habitat within the landscape, the shape of the $\alpha \sim \gamma$ relationship (AGR) summarized by the slope parameter of the log-ratio model still varies a lot (Fig. 3), albeit proportional sampling seems predominant. This variability underlies complex interplays between the level of forest fragmentation and the degree of herbaceous species specialization for forests (Fig. 4). Although the AGR only describes patterns, these patterns may underlie important ecological processes (e.g. community saturation suggests biotic interactions or dispersal limitations) (He et al. 2005) that differ between forest specialists and generalists in response to forest fragmentation. Below, we discuss our main findings in light of the potential underlying ecological processes and their relevance for biodiversity conservation and landscape planning.

Proportional sampling predominates but it hides complex interactions

In general, we found a predominance of linear (i.e. proportional sampling or Type I) AGR (Appendix S6), irrespective of the spatial resolution considered (Table 1), thus supporting former conclusions on the importance of regional processes in shaping local species richness (Cornell & Harrison, 2013; Harrison & Cornell, 2008). Yet, we also found that the prevalence of community saturation was the highest under some circumstances: for forest specialists within highly-fragmented systems and for generalist species within non-fragmented systems. This supports more recent findings on the relative importance of local processes under some environmental circumstances (Michalet et al., 2015). The critical analyses of Gonçalves-Souza, Romero, and Cottenie (2013) and Szava-Kovats et al., (2013), who used the log-ratio method to reanalyze data from 113 and 100 published datasets, respectively, found no prevalence of either unsaturated or saturated communities. In fact, these two meta-analyses concluded that a large proportion of studies produced no discernible patterns (i.e. intermediate and indeterminate cases). Accordingly, our results also show that intermediate and indeterminate patterns between Type I and Type II can contribute a significant proportion in the observed AGR, being predominant in semi-fragmented systems (Appendix S6). Overall, this suggests a gradual shift from either proportional sampling to community saturation (i.e. for forest specialists) or the opposite (i.e. for generalists) as the fragmentation level increases, thus supporting our initial hypothesis of a complex interplay between forest fragmentation and species type (Fig. 1).

Forest fragmentation negatively impacts forest specialists

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Supporting our initial hypothesis for forest specialists (Fig. 1), we found a shift from proportional sampling within non-fragmented systems towards community saturation within highly-fragmented systems (i.e. isolated forest patches within a highly-disturbed matrix of croplands) (Fig. 4b), irrespective of the spatial resolution at which α and γ diversity are measured (Table 1). Within non-fragmented forests, habitat quality is optimal and thus dispersal and recruitment limitations are low for forest specialists. Hence, a proportional increase in the number of forest specialist species co-occurring locally can be observed with the increasing number of forest specialists available from a relatively larger area.

Per contra, highly fragmented forests negatively affect the local establishment of forest specialists, thus decreasing the slope value of the log-ratio model towards community saturation. First, this may reflect a relative increase in competitive exclusion, especially asymmetric competition, when more successful herbaceous plant species gain a progressively greater share of the available resources (Peet & Christensen 1988). In such systems, small-stature forest herb specialists likely suffer from recruitment and persistence limitations in small and/or recent forest patches, due to increased light and mineral nutrient levels that primarily benefit a few generalist tall forbs, e.g. *Rubus fruticosus* agg. and *Urtica dioica,* or creeping woody species e.g. *Hedera helix* in our study. These species contribute to most of the aboveground biomass of the herb layer competing for light (Ma et al. 2018) and may thus competitively exclude smaller-statured forest specialists (Hermy et al. 1999; Verheyen & Hermy 2016) and ultimately decrease herbaceous plant species richness relative to non-fragmented forests (Jacquemyn et al., 2001; Ma et al., 2018). This is especially the case along forest edges, which have been suggested efficient physical barriers against the arrival of forest specialists from neighboring patches (Fischer and Lindenmayer, 2007; Pickett et al., 2001).

Second, in highly-fragmented systems, forest patches are not sufficiently connected to allow most forest herbs to disperse among them, since forest herb species are well known for their low dispersal abilities (Verheyen & Hermy 2001; Vellend et al. 2007). Consistently, we found a tendency towards more forest specialist species accumulating locally as patch age increases (see the effect of covariates from the $\alpha_{FS} \sim \gamma_{FS}$ log-ratio models in Appendix S8), as predicted by the species-time relationship (Rosenzweig & Ziv, 1999) and previous observations in fragmented forests (Jamoneau et al. 2011). In other words, new forest patches are hardly colonized by forest specialists, and it takes even much more time before they spread over the entire forest patch area. Forest specialists within new forest patches thus form scattered founding populations in an

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otherwise generalist-dominated plant community, so that the number of generalists increases faster than the number of forest specialists when increasing the sample area. The observed switch from linear to curvilinear-plateau AGR for forest specialists may thus be explained also in the absence of competitive exclusion (Lawton and Strong, 1981; Mouquet & Loreau, 2003), simply because only good colonizers and very generalist species with a wide ecological niche can quickly colonize a focal area. A similar pattern was reported for calcareous grasslands, where both the size of the species pool and community age influenced local species richness (Pärtel & Zobel 1995). At the same time, populations of forest specialists in older patches may be hardly rescued by immigration and hence, be more exposed to stochastic extirpation (Hérault & Honnay, 2005; Jamoneau et al., 2012), a process potentially contributing to the reported decrease in the slope of the log-ratio model of forest specialists as fragmentation increases.

Forest fragmentation promotes generalist species

The fact that the number of generalist species co-occurring within forest plant communities tend to increase linearly with the number of generalist species available from a relatively larger area inside highly-fragmented systems is consistent with the idea that anthropogenic disturbances as well as edge effects (i.e. the part of a forest patch which is influenced by the surrounding landscape matrix) imposed by agricultural practices may create more favorable conditions for generalist species (Fischer & Lindenmayer 2007), at the expense of forest specialists.

Generalist plant species, that are usually fast-colonizers (Brunet et al. 2011), have been shown to decrease in abundance from the edge to the forest interior, whilst the reverse pattern applied to slow colonizers such as ancient forest plant species (Hardiman et al. 2013). This niche partitioning along edge-core gradients in forests can be explained by the well-known trade-off between survival in deep shade and growth in full light (Hubbell & Foster 1992; Coomes et al. 2009), with the successful penetration of generalists into the forest interior usually limited by unfavorable light conditions (Harper et al., 2005; Hérault & Honnay, 2005). Edge effects have been reported to extend 20 to 50 m (Hérault & Honnay, 2005; Murcia, 1995) and even 100 to 200 m (Laurance et al. 2008; Hardiman et al. 2013) towards the forest interior. In our studied fragmented systems, this means that, to a certain extent, almost all forest patches are edge habitats rather than true forest interior habitats. Generalist species originating from the surrounding landscape are able to colonize edges of forest patches and subsequently migrate towards the patch interior, according to the so-called "biodiversity spillover effect" (Brudvig et al. 2009; Araujo Calçada et al. 2013). This spillover effect is likely more effective in highly-fragmented systems

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where forest patches are more exposed to lime and fertilizer leachates from adjacent croplands, compared to forest patches in the semi-fragmented systems. Moreover, nutrient-rich forests are accompanied by a range of light conditions which is greater than the range of light conditions available in nutrient-poor forests (Coomes et al. 2009), explaining why forests on fertile soils are more species-rich than their counterparts on nutrient-poor soils (Cornwell & Grubb 2003; Laanisto et al. 2008; Coomes et al. 2009).

In contrast with fragmented systems, continuous forest patches in the non-fragmented system represent true forest interior habitats without edge effects, which offer light and soil conditions that are less suitable for generalist species (Jules 1998). The shift from proportional sampling of generalists within highly fragmented systems towards community saturation within non-fragmented systems (Fig. 4c) can thus be explained by the absence of biodiversity spillover effect due to the absence of edge effects. We thus conclude that the shape of the AGR for generalists relates to the spatial distribution of generalist species within the forest patch rather than to biotic interactions: regular over the entire patch, partitioned along the edge-core gradient and randomly clustered in highly-, semi- and non-fragmented systems, respectively.

Conclusion

Our results suggest that forest fragmentation affects the $\alpha \sim \gamma$ relationship by favoring generalist species over forest specialists (Karlson & Cornell 2002; Myers & Harms 2009). The striking different responses to forest fragmentation between forest specialists and generalists suggests that community assembly rules operate differently for these two guilds. In large and ancient forests, high quality habitat combined with the lack of fragmentation allows forest specialists to dominate the herb layer. Conversely, small and/or new forest patches isolated within a matrix of intensively cultivated landscapes are not only hardly colonized by dispersal-limited forest specialists, but also exposed to intense edge effects that allow generalist species to preempt space and resources and subsequently prevent forest specialists from establishment/persistence.

These findings have strong implications for biodiversity conservation and landscape planning, and fuel the single large or several small (SLOSS) debate (Diamond 1975; Simberloff & Abele 1982) by suggesting contrasting impact of forest fragmentation on the community assembly of forest specialists and generalists. Computing the $\alpha \sim \gamma$ relationship across a given landscape and separately between forest specialists and generalists will help to quickly visualize and assess the functioning state, and thus the quality, of forest metacommunities within the focal landscape. This may serve as a diagnostic tool to guide landscape management actions for biodiversity

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conservation, depending on whether one aims at maximizing the total number of species or at maximizing the conservation of patrimonial species such as forest specialists. At a regional scale, the "several small" strategy would indeed increase total species richness per forest patch (Yaacobi et al. 2007; Fahrig 2013), but at the expense of forest specialists by maximizing the proportion of generalist species, whilst the "single large" strategy would primarily benefit forest specialists, that are also the most threatened species in a context of global environmental changes and management intensification of landscapes. Preserving the biggest, most ancient forest patches and maintaining/restoring connectivity between these patches should thus be encouraged in agricultural landscapes to ensure the long-term conservation of forest plant biodiversity, and its associated ecosystem services.

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AUTHOR CONTRIBUTIONS

GD and JL conceived the study and the analytical framework; AJ collected the field data; AA TH, JL, CXGL and SW ran the statistical analyses; EGM conducted all GIS analyses. AA, JL and GD led the writing; all co-authors discussed the results, provided feedback and commented on the initial versions of the manuscript.

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TABLES

Table 1: Outputs from the best candidate model (see main text for the list of candidate models) for each of the two compiled datasets used to analyze the observed variation in the magnitude of the coefficient estimate or slope parameter of the log(γ) variable (i.e. the response variable) in the log-ratio model (see Equation 1 in the main text) of the α ~ γ relationship (AGR): (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90); (2) $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ (n = 180). Linear mixed-effects models (LMMs) were used to relate the response variable against fragmentation level (frag: NF, SF, HF), spatial scale (scale: 1, 2, 3, 4), species type (sp: FS *vs*. FG) and all possible two-way interactions between all three explanatory variables (see the materials and methods section in the main text). Bold values are representing significant (p < 0.05) effects. Grey cells show marginal and conditional R-squared values for each of the three best candidate models.

(1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90)			
	Coeff.	***t***	***p***
*Intercept*_NF	0.042	0.303	0.761
***frag*_HF**	**-0.447**	**-0.343**	**<0.001**
*frag*_SF	-0.102	-0.781	0.434
scale	0.029	0.56	0.575
R^2m/R^2c			0.129/0.129
(2) $\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ (n = 90) & $\alpha_{FG} \sim \gamma_{FG}$ (n = 90)] (n = 180)			
	Coeff.	***t***	***P***
*Intercept*_NF&FS	-0.172	-1.001	0.306
***frag*_HF**	**-0.517**	**-2.176**	**0.029**
***frag*_SF**	**-0.689**	**-2.897**	**0.003**
*sp*_FG	-0.191	-0.802	0.422
frag_HF:sp_FG	**0.748**	**2.225**	**0.026**
frag_SF:sp_FG	**0.583**	**2.923**	**0.003**
R^2m/R^2c			0.173/0.173

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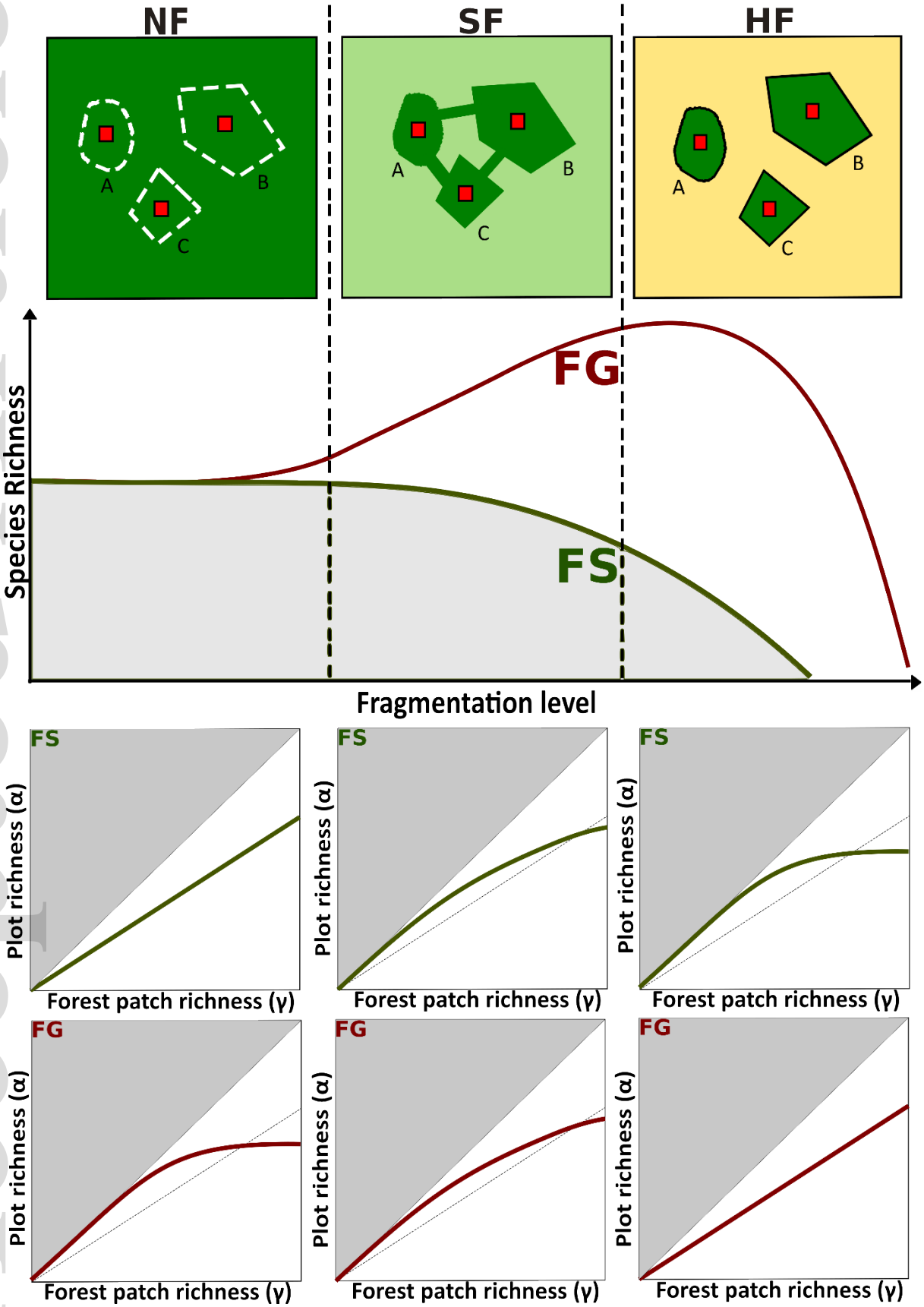

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Figure 1: Schematic figure of the expected effect of forest fragmentation (none, intermediate and high) on the shape of the $\alpha \sim \gamma$ relationship (AGR) for forest specialists (FS) and generalists (FG). For FS in non-fragmented (NF) systems, we expect proportional sampling patterns (Type I) (i.e. α-diversity increases linearly as γ-diversity increases) to predominate while in highly-fragmented (HF) systems, we expect FS to display a predominance of curvilinear-plateau patterns (Type II) (i.e. α-diversity increases until reaching a plateau as γ-diversity increases). For FG, we expect the exact opposite situation as fragmentation increases. In the case of semi-fragmented (SF) systems, where both FS and FG species may locally co-occur, we expect intermediate or even indeterminate patterns to predominate for both FS and FG. For illustrative purpose, three forest patches (A, B and C), being connected or not by corridors (e.g. hedgerows), are depicted within three different types of matrices (forest, pastures with hedgerows, croplands). The less disturbed matrix is a forest matrix with continuous forest patches depicted by the white dotted lines while the most disturbed matrix is an agricultural landscape of croplands with forest patches being isolated from each other. The intermediate matrix is a matrix of pastures with forest patches being connected by hedgerows. The red squares inside the forest patches represent α-diversity while the total patch area represents γ-diversity.

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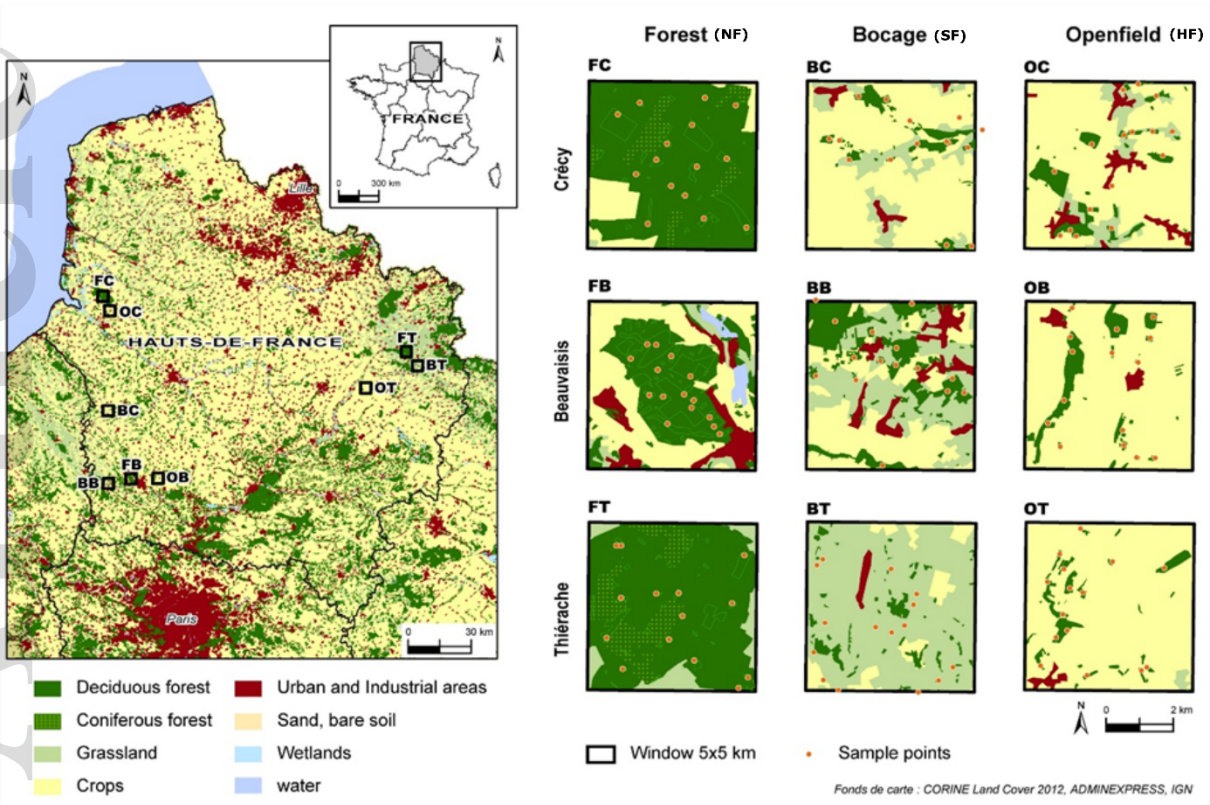

Figure 2: Map of the study area (northern France) covering three different regions (C: Ponthieu and Oise normande, B: Pays de Bray and Beauvaisis, T: Thiérache and Vermandois) with three different types of habitats (Forest, Bocage, Openfield), totaling nine landscape windows with 15 quadrats per window (n = 135 quadrats). Each quadrat is a set of four spatial resolutions, in addition to total patch area, nested within each other: 1m^2; 10m^2; 100m^2; and 1000m^2.

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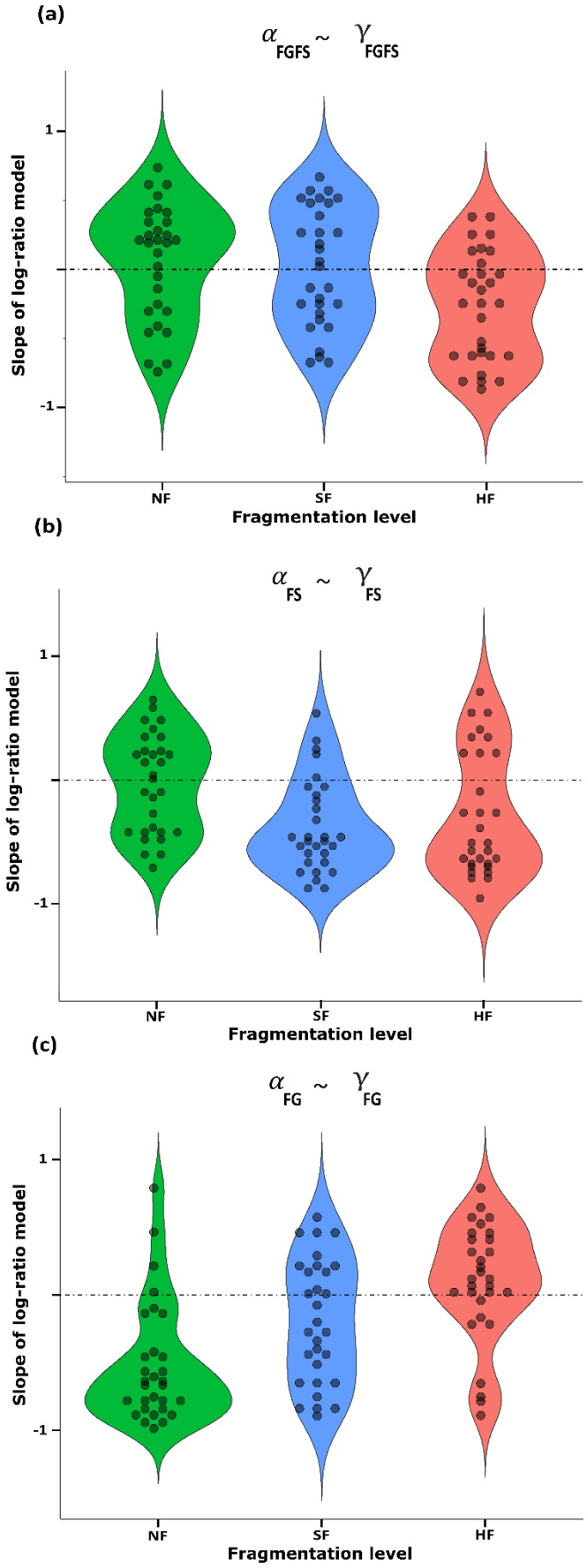

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Figure 3: Variation in the distribution of the coefficient estimate or slope parameter of the log(γ) variable that we extracted from the log-ratio model (see Equation 1 in the main text) and that we used to quantitatively assess the shape of the $\alpha \sim \gamma$ relationship (AGR). Panel (a) represents the distribution of the slope parameter for the combined pool comprising both forest specialists and generalists ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$). Panels (b) and (c) represent the distribution of the slope parameter, separately, for forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) and generalists ($\alpha_{FG} \sim \gamma_{FG}$), respectively. The FS, FG, NF, SF and HF acronyms refer to forest specialists, forest generalists, non-fragmented systems, semi-fragmented systems and highly-fragmented systems, respectively. Green, blue and red colors represent non-fragmented systems, semi-fragmented systems and highly fragmented systems, respectively.

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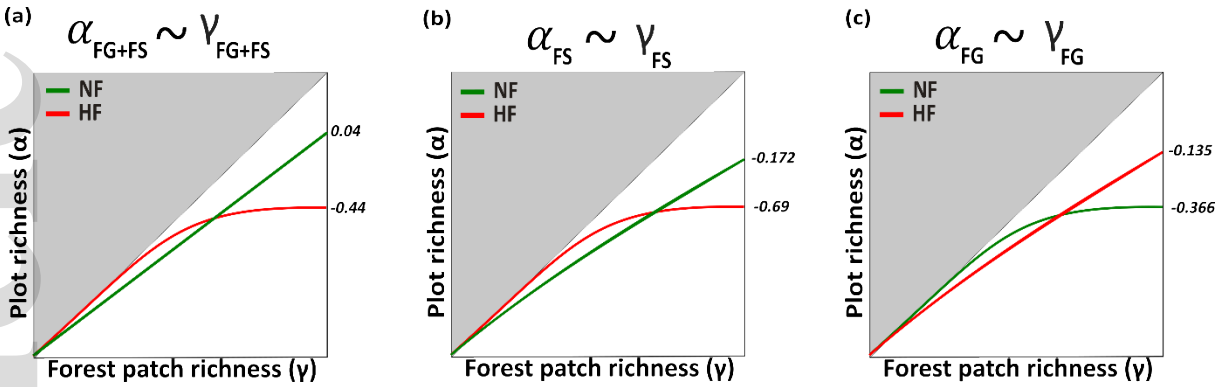

Figure 4: Changes in the α ~ γ relationship (AGR) as a function of fragmentation level. Panel (a) represents the AGR of the combined pool comprising both forest specialists and generalists ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$) showing linear (slope = 0.04) and curvilinear-plateau (slope = -0.44) AGR in non- and highly-fragmented systems, respectively. Panels (b) and (c) represent the AGR for forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) and generalists ($\alpha_{FG} \sim \gamma_{FG}$), separately, with opposite patterns between the two guilds when shifting from non- to highly-fragmented systems. The FS, FG, NF and HF acronyms refer to forest specialists, forest generalists, non-fragmented systems and highly fragmented systems, respectively. Colors and drawings in Figure 5 (i.e. main results) mirror those used in Figure 4.

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Supporting information to the paper

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Appendix S1: Data table (raw data) used in the log-ratio model showing the species richness.

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Appendix S2: Species list.

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Appendix S3: Description of the covariates used in the log-ratio models.

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Appendix S4: Detailed description of the log-ratio model.

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Appendix S5: One sample t-test for the distribution of the 270 slope values & Anova outputs.

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Appendix S6: Based on the coefficient estimate or slope parameter of the log(γ) variable, the $\alpha \sim \gamma$ relationship (AGR) was classified into four types (I, II, INT, IND) for each of the three levels of fragmentation we tested.

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Appendix S7: Outputs from all candidate models.

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Appendix S8: Detailed outputs of two studied cases in the log-ratio models of $\alpha_{FS} \sim \gamma_{FS}$.

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