






# There is room for everyone: Invasion credit cannot be inferred from the species–area relationship in fragmented forests

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## Abstract

**Questions:** Land use change, habitat fragmentation and biological invasion represent major drivers of global change that strongly interact to alter ecosystems. Following the breaking apart of forests into smaller fragments or the afforestation of former agricultural lands, biodiversity experiences drastic changes due to species loss and turnover over time. This leads to two important outcomes, namely extinction debt and invasion (colonization) credit, which both reflect the inertia of the system's response to environmental changes. Our study investigated the following questions:

- Is it possible to infer invasion credit from species–area relationship (SAR) residuals both for native and alien plants?
- Is there any trend linked with the degree of habitat fragmentation through time?

**Location:** Somme, Oise and Aisne departments, northern France.

**Methods:** We analyzed the pattern of SARs' residuals for native and alien vascular plant species separately across nine sets of forest fragments that differ by the landscape matrix they are embedded in (i.e., open field, *bocage*, forest), while considering plant richness, area and age of the 355 forest patches.

**Results:** The relationship between alien and native SARs' residuals is positive across all landscapes, suggesting a lack of invasion credit. Instead, these results support the “rich get richer” hypothesis, that is a high environmental heterogeneity allows colonization by new species, be they native or alien. Interestingly, the relationship between alien and native residuals depends upon fragment age (i.e., time since patch creation) in the most intensively managed landscapes (i.e., open fields). In the latter, recent forest patches are more prone to alien invasion, as a likely consequence of increased alien propagule pressure (i.e., more sources and vectors for alien plants), increased forest invasibility (i.e., disturbance-induced environmental heterogeneity), and decreased matrix permeability (i.e., natives are more dispersal-limited than aliens).

**Conclusions:** Our study provides new insights into alien species ecology, by showing that (i) it is not possible to infer “invasion credit” from the SAR's residuals; (ii) the invasion rate by alien species in forest fragments increases with their native

Giacomo Trotta and Francesco Boscutti contributed equally to this study.

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species richness, and (iii) this relationship depends upon patch age in intensively managed landscapes.

#### KEYWORDS

alien invasion, habitat fragmentation, invasion credit, land cover change, species–area relationship

## 1 | INTRODUCTION

Habitat fragmentation and land use changes are recognized as two major drivers of global change and biodiversity loss (Tilman et al., 1994; Sala et al., 2000; Hanski, 2005; Pimm et al., 2014). Within the next few decades, their impact on biodiversity is predicted to increase (Li et al., 2017). In rural landscapes, fragments result either from the breaking apart of large continuous ancient forests into remote, smaller patches, principally due to forest conversion to agricultural lands (Franklin et al., 2002); or from the recent afforestation of reclaimed agricultural lands by secondary succession or tree planting (Sheffer, 2012). The fragmentation of forests has drastic consequences on species composition and diversity (Hoffmeister et al., 2005). One of the major aftermaths of forest fragmentation is increased edge effects (i.e., by altering environmental conditions), which promote generalist species at the expense of forest specialists (Almoussawi et al., 2020). This is mainly caused by the gradient of environmental conditions (e.g., increasing light, availability of nutrients and agrochemicals) from the forest core to the outer edge (Chabrierie et al., 2013). Along this ecotone niche partitioning occurs, allowing the coexistence of more species (i.e., compared with the forest interior) especially non-forest species (Chabrierie et al., 2013; Rejmánek, 2014; Richardson et al., 2014; Wagner et al., 2017). Furthermore, a lack of connection between fragments can disrupt the dispersal network of native plants, especially for dispersal-limited specialists, thereby exposing forest fragments to a higher risk of colonization by good dispersers, such as many alien species (Honnay et al., 2002; Matthies et al., 2004; Tanentzap et al., 2010). Moreover, disturbance associated with agricultural land use and management can increase the invasibility of forest edges, and facilitate the dispersion of alien plant diaspores across landscapes (e.g., propagules carried by vehicles or domestic animals) (Boscutti et al., 2018; Pellegrini et al., 2021).

Time is also a central issue in plant invasion, for instance, the residence time of alien species, expressed as the time that a species has been in its introduced range often interacts with propagule pressure to set its final spread into the landscape (Pyšek & Jarošík, 2005; Wilson et al., 2007). In turn, the invasibility of recipient habitat might also greatly change over time, due to disturbance regime and successional biotic filters. It has been already demonstrated that time since disturbance determines the reduction of ruderal and alien species in lowland forest fragments (Della Longa et al., 2020) while in secondary successions aliens have been shown to rapidly decrease in

richness during the early stages of succession (Boscutti et al., 2017; Mosanghini et al., 2023).

In this context, plant invasion, habitat fragmentation, land use change, and time since disturbance are expected to strongly interact, triggering local species extinction and/or immigration, thereby causing immediate and delayed changes in community composition and biodiversity (Jackson & Sax, 2010; Liu et al., 2019). Delayed changes in particular have been conceptualized through the “extinction debt” and its counterpart, the “colonization credit,” also known as “invasion credit” or “immigration credit” (Jackson & Sax, 2010). There is no “extinction debt” when long-living species that initially survive despite no longer suitable environmental conditions later go extinct without any further environmental change, causing time-delayed species loss (Tilman et al., 1994; Vellend et al., 2006; Kuussaari et al., 2009; Dullinger et al., 2012; Hylander & Ehrlén, 2013; Halley et al., 2017). Hence, it refers to the future biodiversity cost of current habitat destruction that will be paid (Tilman et al., 1994). Similarly, the invasion credit represents the time-delayed species gain due to the progressive establishment of new species into an extant community (Jackson & Sax, 2010). In fact, when a forcing event occurs (e.g., habitat fragmentation), we expect a long-term colonization trend (Vilà & Ibáñez, 2011) from the regional species pool, due to the availability of new niches. “Extinction debt” and “invasion credit” are considered consequences of the inertia of the system responding to disturbance while extinction and colonization are the corresponding processes (Tilman et al., 1994; Jackson & Sax, 2010).

According to Kuussaari et al. (2009), an “extinction debt” can be predicted relying on island biogeography theory (MacArthur & Wilson, 1963, 1967) by comparing the observed richness in stable and recently fragmented patches. This is possible by using the species–area relationship (hereafter SAR), that is, the relationship between the number of species and the sampled area. A similar approach might be suitable to predict the “invasion credit” (i.e., considering colonization by native and alien species) but, so far, studies about the application of SAR in the invasion context are few and mainly focused on testing island biogeography theory and the consistency between alien and native species patterns (Hulme, 2008; Blackburn et al., 2016; Chiarucci et al., 2021). On the other hand, SAR is considered a fundamental pattern in ecology (Schoener, 1976; Scheiner, 2003; Scheiner et al., 2011) and it has been used in several studies to understand how biodiversity changes when habitat is lost or fragmented into smaller island-like habitats (Diamond, 1975; Hanski et al., 2013; Fahrig, 2017).

As a novelty, we here extend the use of SAR to evaluate the potential invasion credit of small forest patches. We underline that invasion credit can refer to both alien and native species. In this study, our main aim is to test whether invasion credit of alien plants can be inferred from the residuals (i.e., the difference between the actual value and the value predicted by the model) of models of the native and alien SARs. We decided to use the residual to nullify the area effects (i.e., independence from spatial extent) and investigate alien and native response to habitat heterogeneity (Hulme, 2008). Our hypothesis is that the higher the negativity of the native residual, the higher the invasion credit of alien species (Figure 1). In other words, we ask whether there is a proportionally higher number of alien species within a forest patch with a lower number of observed natives. Basically, we think that a lower number of native species, as measured by negative residuals of native species, provides a measure of distance from the complete niche occupation by native species and a higher number of niches available for alien species, leading to an invasion credit by alien plants. Furthermore, we want to determine whether this relationship depends upon the age of forest fragments (i.e., compare patches at the same successional stage) and/or the permeability of the landscape matrix into which these fragments are embedded. We expect our results will contribute to the understanding of forest invasion processes, providing new insight into the conservation and management of forest patches embedded in intensive or extensive agricultural landscapes.

## 2 | MATERIALS AND METHODS

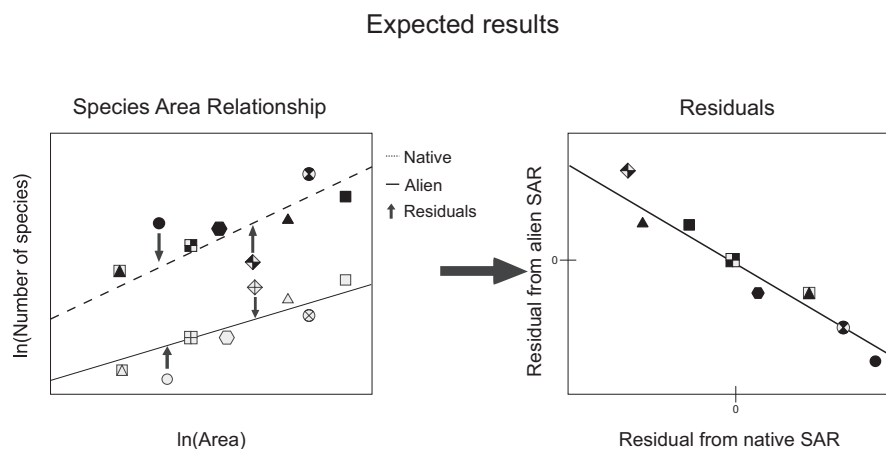
### 2.1 | Study areas

The study was conducted in three administrative departments of northern France (i.e., Oise, Somme, Aisne; 49°25'–50°11' N, 1°25'–3°55' E; alt. 60–220m). The climate is oceanic with an annual mean temperature of 10°C, annual rainfall of 700mm and evapotranspiration of 711mm. The geological substrate mainly consists of Cretaceous chinks, often covered by Quaternary deposits. The area has been widely converted into agricultural land. Only a few large forests (>1000ha) are present and are represented by three ancient

forests (i.e., forest of Crécy, forest of Parc Saint-Quentin, forest of Nouvion); the rest of the forest area is highly fragmented, with patch range between 0.5 and more than 50ha (Jamoneau et al., 2012). These forest fragments mostly result from recent afforestation of former agricultural lands, less frequently from the fragmentation per se of ancient forests (i.e., historical maps were used to establish this). Often, these forest patches are surrounded by extended croplands that are intensively cultivated for cereals, oil seed rape and sugar beet (hereafter “open field,” referring to croplands landscape). In some areas, however, grasslands dominate the landscape, still with some small croplands used for less intensive agriculture, and usually enclosed by hedgerows (hereafter “*bocage*”). Forest patches are mainly small private (coppice) woodlands that are either unmanaged or lightly managed by their owners, for recreational purposes (mainly hunting) and/or fuel production. Only patches included in big forest tracts are systematically managed as high forest systems for timber production.

Three sets of 5km×5km landscape windows were selected in each of the three departments: one in each landscape type (i.e., open field and *bocage*), where all forest fragments were considered connected by dispersal events, hence forming a single metacommunity (Leibold et al., 2004); and a third set in a large, non-fragmented forest (hereafter “forest”). The extent and age of the forests chosen are: forêt de Crécy, presence attested since the Iron age, 4795 ha (i.e., Somme department); forêt du Parc Saint-Quentin, presence attested since 3rd century, 833ha (i.e., Oise department); forêt du Nouvion, presence and continuity attested before the 5th century AD, 4088ha (i.e., Aisne department). In the non-fragmented forest, virtual patches (hereafter “fake-forest fragments”) were manually created within each forest simulating in number, size and shape those of the patches found in the open-field and *bocage* landscapes. In total nine landscapes were selected, three from open-field matrix, three from *bocage* and three from forests. A total of 355 fragments were surveyed: 89 from open field, 154 from *bocage* and 112 from forest landscapes, similar between each landscape in terms of variation of size and distribution (i.e., mean area size 5.31ha, minimum size 0.05 ha and maximum size 174ha). For further details see Jamoneau et al., 2012. A summary of the plot disposition across the country is presented in Appendix S1.

**FIGURE 1** Expected result according to the invasion credit hypothesis. We assume that the lower the residuals of the native's SAR, the higher the alien's residuals (i.e., higher invasion credit). Arrows in the first window show the residual between the expected value (i.e., regression line) and observed value (i.e., points). Each point has a different shape to link its residuals to the graph on the left. The dotted line refers to the native's SAR while the continued line refers to the alien's SAR.



## 2.2 | Data collection

### 2.2.1 | Flora of forest patches

A complete species list of all occurring vascular plants was compiled for each of the 355 patches (i.e., presence/absence data). Flora surveys were repeated in spring (April–May) and in summer (June–September) in 2007 and 2008. Intraspecific taxa and planted ornamental species were omitted. Species aggregates of critical taxa were incorporated as a single taxon (e.g., *Taraxacum officinale* agg.). The surveys were conducted by a team of the University of Picardie. Alien status was assigned according to a checklist (Lambinon et al., 1995) and the regional checklist provided by the Conservatoire botanique national de Bailleul (Desse, 2021). A table with species status and frequency is available in Appendix S2.

### 2.2.2 | Fragment and landscape characterization

The area of each forest fragment was calculated using GIS software (ArcGis v.8.3). Changes in forest extent across time were analyzed using historical Cassini maps (drawn ca 1780, error 80m), French military “Etat Major” maps (ca 1880, 36m), IGN maps (ca 1955, 6m) and aerial photographs (2002). Patch age was estimated using the median time between the map on which it was first represented and the immediately preceding map, hence four possible ages: 26 (1955–2002), 87 (1880–1955), 172 (1780–1880) and 300 (<1780) years. Given that a single forest fragment can consist of a mosaic of patches with different ages, an age index for each fragment  $i$  was computed as follow:

$$A_i = \sum p_t \ln(\text{age}_t),$$

where  $p_t$  is the proportion of patch  $i$ , which was present at time  $t$ .

## 2.3 | Data analyses

### 2.3.1 | Theoretical framework

The Independent Species Richness Relationship derived from Scheiner's (2003) “Type-IV” curve (Figure 1) is usually utilized in studies dealing with island samples or island-like habitats (e.g., lakes, mountain tops, isolated forest) (Scheiner et al., 2011; Dengler et al., 2020). The two mathematical functions most widely used for the shape of the species–area curve are Gleason's exponential curve (1925) and the power curve of Arrhenius (1921). They can be synthesized as follows:  $S = z \ln(A) + c$  (Gleason, 1925) and  $S = cA^z$  where  $S$  is the number of species,  $A$  is the area,  $c$  is the intercept and  $z$  represents the slope of the linear model (Scheiner, 2003). More specifically,  $c$  represents the number of species per unit area and  $z$  the increment of species per unit area (Arrhenius, 1921; Gleason, 1925; Lomolino, 2001). Both constants ( $c$  and  $z$ ) need to be empirically calculated.

Once the best-fitting model (i.e., lower AIC and higher  $R^2$ ) is obtained, it is possible to calculate the SAR model's residuals (i.e., the difference between observed and predicted values). They are a useful tool because they reflect the actual floristic richness and nullify area effects among floras, making them comparable (Fattorini et al., 2017).

### 2.3.2 | Statistical approach

The statistical analyses were conducted based on a two-step procedure: (i) testing the residuals across the nine landscapes and three environments and (ii) testing for the relationship between alien and native SAR's residuals and time since the last disturbance event (i.e., age of the forest fragments).

For each fragment, we calculated total, native and alien species richness (number of species). We tested Gleason and Arrhenius models for each landscape, retained the average best-fitting model based on the lower AIC value and higher  $R^2$ , and created the best SAR curves for each of the nine landscapes. All statistical analyses were performed with the statistical software R 3.6.3 (R Core Team, 2020). The models were calculated using the *sars* package (Matthews et al., 2019). We further selected the models' residuals as the difference between the observed and the predicted value of the number of species for each fragment. Residuals were computed for total, alien and native species. The residuals from native SAR models were used as predictors to explain variation in residuals from alien SAR models. To achieve this outcome, linear models were calculated for alien and native plant residuals for each of the nine landscapes. All the models were represented with the *ggplot* graphic tool (Wickham, 2016).

Interactions between alien/native residual models and landscape (i.e., open field, *bocage*, forest) were tested using linear mixed-effects models (LMMs) and the *nlme* package (Pinheiro et al., 2021), considering the Department as random effect. The same approach (LMM) was applied to test separately, within each landscape type, the interaction between alien/native residual model and patch age (i.e., time since the fragmentation event had created the patch). Graphic results were represented with the R package *effects* (Fox & Weisberg, 2018).

## 3 | RESULTS

In total, the 355 patches contained 625 vascular plant species, of which 515 were natives (N) and 110 were aliens (A: 17.7% of the total).

### 3.1 | SAR modeling

The mean  $R^2$  value was 0.669 (Table 1). The Arrhenius power function model most often gave the best fit with our observations. SAR

was better predicted for native than for alien species (mean  $R^2$  of 0.763 and 0.62 respectively). SARs are shown in Figure 2 for the nine landscapes and for alien and native species separately, showing consistent trends. Native richness increases more than alien richness with increasing area.

### 3.2 | Relationships between predictive errors of native and alien SARs

We found a strong positive relationship between native and alien SAR's residuals (Figure 3). This means that increasing the value for native residuals (i.e., more native species than predicted by the SAR) increased the value for alien residuals. The relationship was significant ( $p$ -value < 0.05) for six out of the nine models and explained between 10% and 69% of the total variance.

### 3.3 | Relationship with landscape type and patch age

The relationship between alien and native residuals showed a non-significant interaction with landscape type considered (i.e., open field, *bocage* or forest:  $F$ -value = 0.247,  $p$ -value = 0.781). The same relationship was found even when pooling open-field and *bocage* fragments in contrast to "fake fragments" (i.e., forest) ( $p$ -value = 0.621). Interestingly, results shown that the alien–native residuals relationship exhibits a significant interaction with fragment age (i.e., age index) in open-field landscapes ( $p$ -value < 0.05), but not in the *bocage* and forest landscapes ( $p$ -value = 0.130 and 0.697 respectively). The use of age as a factor allowed us to evaluate the relationship between residuals of aliens and natives in patches at the same successional stage. Indeed, recent patches should show ongoing native species extinctions or can be considered landscapes which are still changing. In open-field patches, a gradual increase in fragment age exacerbates the positive relationship between alien and native residuals. Indeed, Figure 4 shows that in recent patches the alien residual value remains near zero (i.e., no distance between the observed value and expected value). In particular, recent forest patches did not show any trend between native and alien residuals, while when patch age increased, the relationship became more and more positive (i.e., the slope increased; Figure 4).

## 4 | DISCUSSION

We found strong evidence of a direct relationship between alien and native residuals from SAR models, offering new insights into the invasion credit hypothesis (Jackson & Sax, 2010). In particular, our results showed that where native species richness was higher than expected (positive model residuals) the number of alien species was also higher than expected, refuting our initial hypothesis of a progressive replacement of natives by aliens. Conversely, our finding

supports the "rich get richer" hypothesis (Rejmanek, 2003; Stohlgren et al., 2003), consistent with the habitat heterogeneity hypothesis (MacArthur & MacArthur, 1961; Pianka, 1966; Vivian-Smith, 1997), stating that an increase in habitat diversity also leads to an increase in species richness due to the availability of physical space and resources. This can be true for both alien and native species and is related to their establishment ability. This is also consistent with a high propagule pressure and the mass effect derived from metacommunity ecology, declaring that species' dispersion relies on the species richness of the fragment's surroundings (i.e., species flow from areas of high success to less favorable areas) (Shmida & Wilson, 1985). This increases the chance for species to become established (Stohlgren et al., 1999). However, we found that fragment age did influence the relationship between alien and native residuals only when forest fragments were embedded in an intensively managed agricultural landscape (i.e., open field).

Alien species pools (including all non-native plants) were consistent with previous studies on the European forests, with 17.7% of the species represented by non-native taxa (e.g., in Wagner et al., 2021, alien species in northern France's forest represented 20% of the total). The SARs of alien and native species were consistent with those found by Scheiner (2003) using type-IV curves, indicating significant positive species–area relationships. Despite a general consistency between linear models of SARs for alien and native species, a better fit was observed for native species when using the Arrhenius model, with aliens showing a constantly lower proportion of variance explained by the models, as expected by their more uneven distribution across sites (e.g., Chiarucci et al., 2012; Guo et al., 2021). This can be true due to stochastic invasion events: any alien species can establish in a forest fragment whenever it can disperse and reach a suitable habitat patch. This is also reflected by the significantly lower richness of alien species compared with native species (mean value per patch was 2.49 for alien and 69.53 for native).

### 4.1 | Relationships between native and alien SAR residual: "Invasion credit" or "rich get richer"?

Analyzing the relationships between alien and native SAR residuals we found an unexpected trend, which did not confirm our invasion credit hypothesis: high negative native residuals do not correspond to high positive alien residuals. This indicates that it is not possible to infer an invasion credit, defined as natives replaced by aliens, from SAR residuals. Our results thus do not support the "barrier effect" of biodiversity against biological invasion (Levine & D'Antonio, 1999; Kennedy et al., 2002) at the fragment scale. Instead, the positive relationship between alien and native residuals suggests that where there is a surplus (or a deficit) of natives compared with the expected value (i.e., the species richness inferred by the SAR model), a surplus (respectively, a deficit) in alien richness was also observed. This is consistent with a growing body of literature (Ordóñez & Olf, 2013; Bjarnason et al., 2017; Bajocco et al., 2019; Kortz & Magurran, 2019)

TABLE 1  $R^2$  values of the two SAR models tested, Gleason and Arrhenius, for each landscape (rows) and region (columns).

	Oise			Somme			Aisne		
	Gleason	AIC	Arrhenius	Gleason	AIC	Arrhenius	Gleason	AIC	Arrhenius
<b>Openfield</b>									
All species	0.7***	261.5	0.81***	0.66***	269.5	0.74***	0.64***	258.2	0.77***
Natives	0.7***	255.5	0.8**	0.67***	263.3	0.74***	0.64***	254.2	0.76**
Aliens	0.55***	135.4	0.77***	0.19***	175.2	0.32***	0.44***	124.8	0.73***
<b>Bocage</b>									
All species	0.8***	553.7	0.88***	0.81***	277.8	0.83***	0.58***	532	0.65***
Natives	0.81***	542.6	0.87***	0.81***	270.2	0.83***	0.59***	527.3	0.65***
Aliens	0.56***	327.6	0.65***	0.69***	150.8	0.8***	0.01°	304.2	0.05°
<b>Forest</b>									
All species	0.79***	383.6	0.83***	0.64***	266.8	0.7***	0.74***	336	0.76***
Natives	0.79***	377.9	0.82***	0.62***	262	0.65***	0.74***	332.9	0.75***
Aliens	0.63***	199.1	0.87***	0.49***	159.6	0.86***	0.44***	149.4	0.53***
<b>Openfield</b>									
All species	0.7***	261.5	0.81***	0.66***	269.5	0.74***	0.64***	258.2	0.77***
Natives	0.7***	255.5	0.8**	0.67***	263.3	0.74***	0.64***	254.2	0.76***
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Note: In bold we highlighted the highest value between the two models.  $p$ -Value is indicated as: \*\*\*, 0.001; \*\*, 0.01; \*, 0.05; °, 0.1; °, 1.



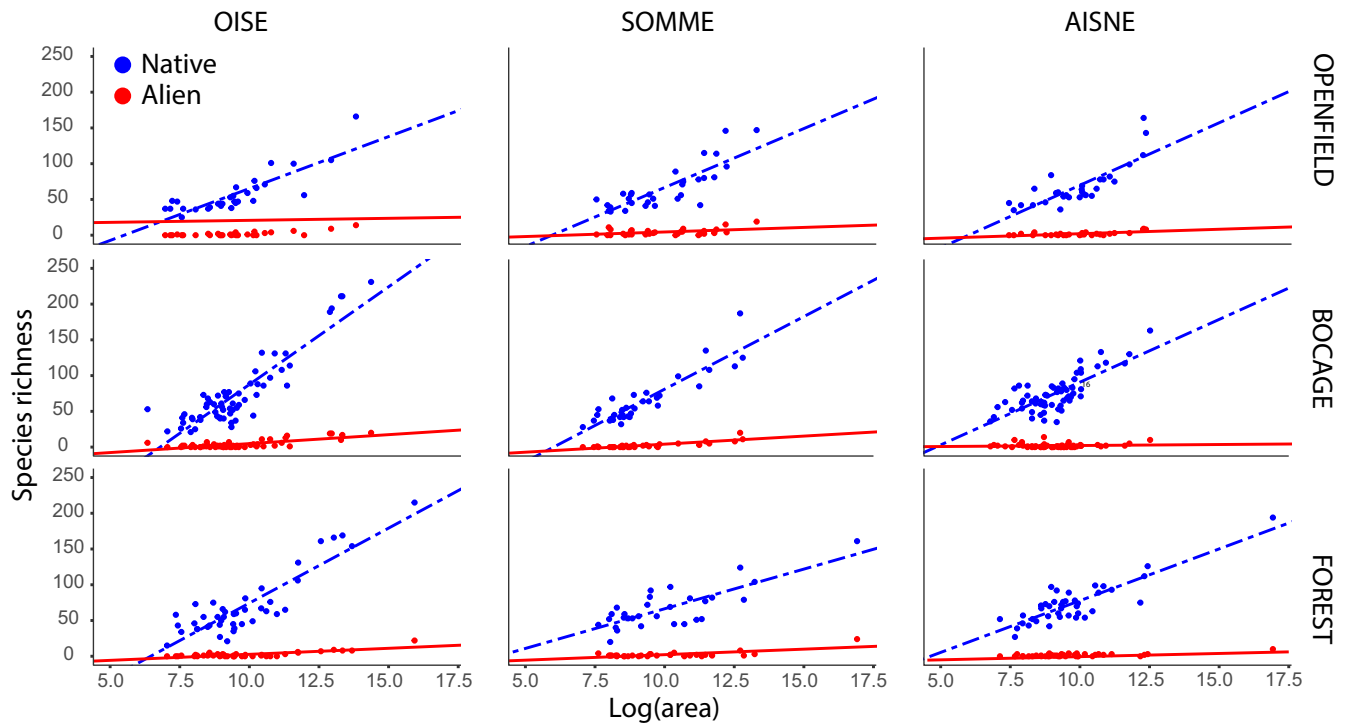


FIGURE 2 Alien (solid red line) and native (dashed blue line) SAR model (using the Arrhenius model to make the nine landscapes comparable).

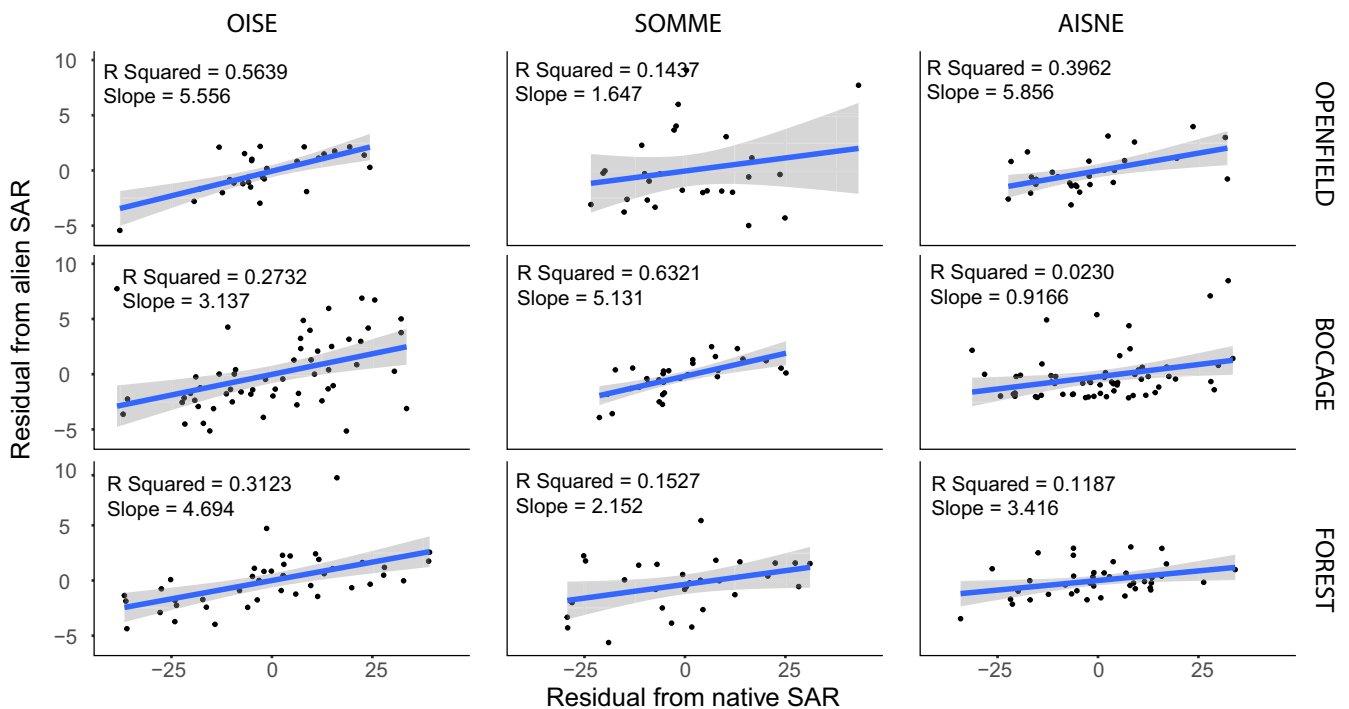
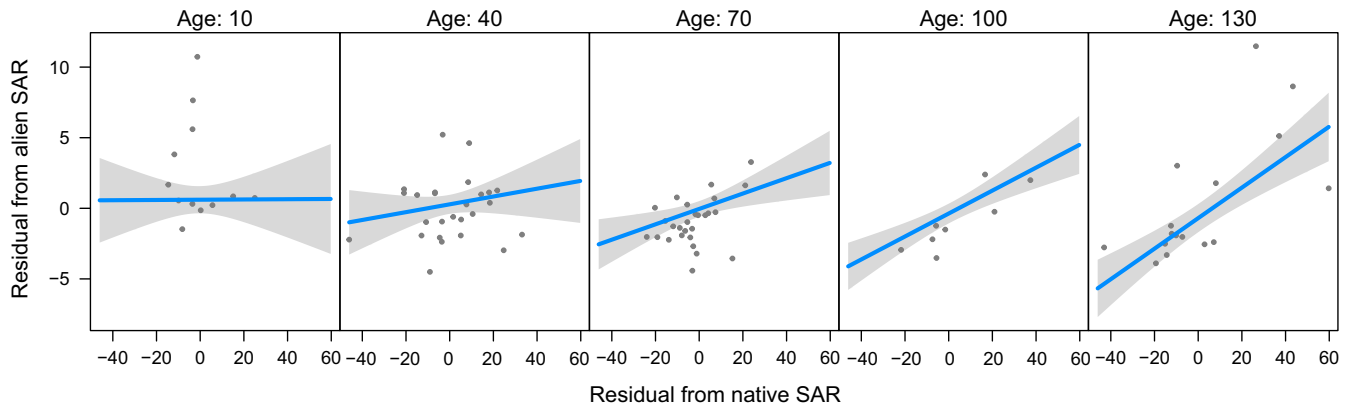


FIGURE 3 Relationship between alien and native SAR residuals from Arrhenius models. In the upper left corner is shown the  $R^2$  value of each linear model. Shaded area is the 95% confidence interval.

which found that a high alien richness is associated with a high native richness, often following a disturbance. Furthermore, while native woodland species are often dispersal-limited, successful aliens are usually characterized by an effective dispersal strategy (Herm

et al., 1999; Jongejans et al., 2008; Murray & Phillips, 2010). Among aliens, wind disperser species (e.g., *Erigeron canadensis*, *Juncus tenuis*, *Symphotrichum lanceolatum*, *Galinsoga quadriradiata*) are important contributors to the community as part of the dispersal-assembled



**FIGURE 4** Effects plot of the interaction between patch age (expressed as age index of each patch) and the relationship between alien and native SAR residuals in open-field landscapes. Shaded area is the 95% confidence interval. The model included the age index as a predictor and not the age classes.

pool. In addition to aliens that are effective wind dispersers, also many generalist species contribute to the assembly of the final alien pool. The positive relation was also found in Stark et al. (2006) and Hulme (2008) where areas that were bad for natives were even worse for aliens. This is also consistent with Stohlgren et al. (2003) and Guo et al. (2021) and supports the “rich get richer” hypothesis. This result indicates that local communities, if not saturated, can accumulate immigrant species over time, be they natives or aliens.

Contrary to our expectation, the native–alien species relationship was not affected by the landscape matrix. This is surprising since several studies have shown that highly disturbed landscapes, such as agricultural lands, promote alien invasion (Catford et al., 2012; Wagner et al., 2017; Boscutti et al., 2018; Pellegrini et al., 2021). In our study, alien species do not replace native species but accumulate at the same time as they do over the course of secondary succession. This can be considered a “proportional” colonization, and might be linked to the non-invasive status of many forest aliens occurring in the patches, which were not able to replace and stop the ingression of other native and alien species, hence enriching the habitat rather than depauperating it.

Alien species are predominantly generalists (Steyn et al., 2017) and, compared with forest specialists, are more light- and nutrient-demanding (Rejmanek & Richardson, 1996; Green et al., 2004; Leishman et al., 2007; Van Kleunen et al., 2010). This implies that in “open” landscapes the ecological conditions, due to the edge effect, recent disturbance and diaspora pressure from the matrix, are favorable for the establishment of generalist species. In contrast, in unfragmented forest specialist species should dominate more. This might explain the flattened slope that we observed.

## 4.2 | Relationship between alien SAR's residual and patch age

Interestingly, we found a significant effect of patch age (i.e., time since patch creation) on the relationship between alien and native

residuals only in open-field landscapes (i.e., where the matrix is submitted to intensive agriculture). In these landscapes, as native residuals change, alien residuals remain constant, suggesting that recent forest patches are rapidly colonized by alien species (i.e., alien species reach the expected value derived from the SAR rapidly) while the number of natives is much more variable, probably due to contrasted colonization abilities (Lami et al., 2021). We see three interacting factors shaping the alien/native assemblages along the observed succession (from recent to ancient forest patches): (i) patch invasibility, (ii) species' dispersal limitations and (iii) propagule pressure and its relation with alien species' residence time.

Firstly, disturbance intensity has been repeatedly shown to increase habitat invasibility, by freeing space and resources (Davis et al., 2000). It is obvious that invasibility is higher in recent than in ancient forest patches, since the former result from secondary succession on reclaimed agricultural lands. The open tree canopy, the lack of a litter layer and the soil fertility inherited from former agricultural practices allow many light- and nutrient-demanding species, including many alien species, to easily establish, in contrast with light and soil conditions offered by ancient forest patches (Woods, 1997; Catford et al., 2012; Thomas & Moloney, 2015; Sardans et al., 2017; Song et al., 2017; Della Longa et al., 2020). Moreover, compared to *bocages*, open fields are the landscapes with the greatest management intensity favoring the spread of alien plants (Pellegrini et al., 2021). Mechanical operations and agrochemical sprays represent recurrent disturbances of forest edges, allowing ruderal species such as most alien species to establish and persist (Chabrerie et al., 2013).

Secondly, dispersal limitations are likely to play a major role. Compared with generalist species, ancient forest species and forest specialists in general are well known to be dispersal-limited (Hermy et al., 1999; Kimberley et al., 2013). This is especially true in fragmented systems, and even more in the open-field landscape where the matrix is almost impermeable to forest specialists (Jamoneau et al., 2012). Many invasive species are generalists with a persistent



seed bank and adaptations to long-distance dispersal (e.g., wind dispersal), which may confer them a head start over native generalists (Lloret et al., 2004; Vilà & Gimeno, 2007). Moreover, they often can be spread by non-standard means of dispersal such as agricultural vehicles (Von der Lippe & Kowarik, 2007). Among the studied landscapes, the open fields exhibit the highest density of roads and tracks, which can act as effective corridors for many generalist species (Decocq et al., 2021), and support the heaviest traffic. As a result, aliens may preempt space and resources at the very beginning of the secondary succession (Mosanghini et al., 2023), followed by native generalists and, later in the course of succession, by forest specialists helped by animal dispersion.

Thirdly, a high propagule pressure has been shown to be a crucial attribute of many invasive species, which enables them to increase colonization success of natural habitats (Tilman, 2004; Lockwood et al., 2005). Compared to forest and *bocage* landscapes, open fields support more villages and isolated farms with gardens, where a number of alien species are usually cultivated as ornamentals. Moreover, the more numerous road verges and marginal lands can act as occasional habitats for these aliens, thereby contributing to increasing the propagule pressure on surrounding forest patches (Boscutti et al., 2022). In this light, young forest fragments occurring in the landscape might also provide some more opportunities for species to spread into the landscape, affecting their residence time. Our result suggests further analyses aimed at testing the role of young disturbed forests in the landscape as potential sinks and sources of alien plants, probably able to shorten the overall time needed by new alien species to spread in new areas.

## 5 | CONCLUSION

Our findings indicate that the study of species–area relationships does not support an invasion credit hypothesis either for forest patches embedded in agricultural landscapes or for unfragmented forest. However, we observed that such relationships might be age-dependent.

The results were consistent across the considered landscapes showing a positive relationship between native and alien species' residuals (from the SAR models) supporting the “rich get richer” hypothesis (Stohlgren et al., 2003). In general, these results suggest that environmental heterogeneity promotes high biodiversity, with a constant proportion of alien species. Moreover, this concept seems to be consistent across landscapes.

We also found a significant interaction between alien/native residuals and forest patch age, but only for patches included in an open-field matrix. This landscape seems the most favorable to invasion, which especially affects recent patches, as a likely response to higher disturbance, higher propagule pressure and altered dispersal networks.

The present findings have important implications for establishing future conservation programs. In particular, our study highlighted

how environmental heterogeneity contributes to the spread of alien species and why more species-rich environments have a high probability of alien richness.

## AUTHOR CONTRIBUTIONS

Alessandro Chiarucci and Guillaume Decocq conceived the ideas and designed methodology; Aurélien Jamoneau, Guillaume Decocq and Alessandro Chiarucci collected all the data; Giacomo Trotta and Francesco Boscutti analyzed the data; Giacomo Trotta, Francesco Boscutti and Alessandro Chiarucci led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## DATA AVAILABILITY STATEMENT

The dataset is available at Mendeley Data, V1, “There is room for everyone: Invasion credit cannot be inferred from the Species–Area Relationship in fragmented forests”, doi: [10.17632/6htzhvp2nk.1](https://doi.org/10.17632/6htzhvp2nk.1).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Localization and distribution of the 355 patches.

**Appendix S2.** List of species found with the corresponding frequency.

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