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RESEARCH ARTICLE

# Regional invasion history and land use shape the prevalence of non-native species in local assemblages

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## Abstract

The ecological impact of non-native species arises from their establishment in local assemblages. However, the rates of non-native spread in new regions and their determinants have not been comprehensively studied. Here, we combined global databases documenting the occurrence of non-native species and residence of non-native birds, mammals, and vascular plants at regional and local scales to describe how the likelihood of non-native occurrence and their proportion in local assemblages relate with their residence time and levels of human usage in different ecosystems. Our findings reveal that local non-native occurrence generally increases with residence time. Colonization is most rapid in croplands and urban areas, while it is slower and variable in natural or semi-natural ecosystems. Notably, non-native occurrence continues to rise even 200 years after introduction, especially for birds and vascular plants, and in other land-use types rather than croplands and urban areas. The impact of residence time on non-native proportions is significant only for mammals. We conclude that the continental exchange of biotas requires considerable time for effects to manifest at the local scale across taxa and land-use types. The unpredictability of future impacts, implied by the slow spread of non-native species, strengthens the call for stronger regulations on the exchange of non-native species to reduce the long-lasting invasion debt looming on ecosystems' future.

KEYWORDS
biological invasion, invasion debt, land use, local assemblages, residence time

## 1 | INTRODUCTION

The expansion and intensification of global trade and transport have resulted in increasing rates of intra- and intercontinental biotic exchange (Capinha et al., 2023; Hulme, 2021; IPBES, 2023; Seebens et al., 2017). While most established non-native species are currently inconspicuous additions to regional biotas, a sizable minority causes considerable ecological damages

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(Diagne et al., 2021; Kumschick et al., 2015; Vilà et al., 2011). Documenting, understanding, and controlling biological invasions have hence become key themes in environmental science and policy (IPBES, 2023; Pyšek et al., 2020).

Knowledge of the distribution of non-native species has recently improved substantially for several taxonomic groups (e.g., vertebrates and vascular plants) across most regions of the globe (Dawson et al., 2017; Dyer et al., 2017; Pyšek et al., 2020; Seebens et al., 2017; van Kleunen et al., 2015). However, while this documentation and related analyses mostly focus on the regional scale, the impact of non-native species on native biota is mainly driven by interactions in local assemblages (Pyšek et al., 2017; Vilà et al., 2011). Understanding the process of non-native species spread into and across local assemblages within a region is consequently important for both the understanding and management of biological invasions. Invasion by an introduced non-native species usually starts from small and often initially ephemeral populations near introduction sites. After the species survives and reproduces, resulting in established populations, it may spread across the entire potential range of the non-native species within the new region (Duncan, 2021; Flores-Moreno et al., 2016; Rouget et al., 2016). Until the colonization of all suitable sites, there is a potential latent increase in assemblages invaded representing the “invasion debt” of that region (Essl et al., 2011; Robeck et al., 2024; Rouget et al., 2016). The magnitude of this invasion debt, as well as the time until it is “paid off,” is key to evaluating possible future impacts of biological invasions. The payoff times are likely to be specific to the identity of the non-native species, the ecosystem type and their combinations. Despite their theoretical and applied value, comprehensive estimates of means or approximate magnitudes of the time that established non-native species need to reach distributional equilibrium are rarely available.

Several studies have demonstrated that non-native species are more frequently found in human-disturbed environments (Chytrý et al., 2009; Chytrý, Maskell, et al., 2008; Didham et al., 2007; Kalusová et al., 2017; Liu et al., 2023), likely because disturbances temporarily increase resource availability and decrease competition with native species (Davis & Thompson, 2000; Lebbink et al., 2022; MacDougall et al., 2013). Human land use (LU) is a major cause of ecosystem disturbance and can facilitate the accumulation of non-native species in local assemblages, although with considerable variation across LU-types and taxonomic groups (Liu et al., 2023). However, we still need to systematically determine whether the currently observed higher frequency of non-native species in assemblages under human use reflects higher rate or eventual magnitude with which these assemblages are invaded. In fact, empirical evidence from various case studies suggests that the number of habitat types occupied by non-native species tends to increase with residence time, leading to larger and more widespread source populations within a region (Alexander et al., 2011; Hejda et al., 2015). As a consequence, the currently lower occurrence and abundance of non-native species in natural or near-natural ecosystems (Liu et al., 2023) may in part result from slower spread into these ecosystems, and hence, a longer lasting invasion debt compared to human disturbed ones.

Here, we provide a global-scale analysis of the links between residence time of non-native species, their occurrence in local assemblages, and LU for three taxonomic groups: birds, mammals, and vascular plants. We combined five different databases. The first three databases provided regional-scale non-native species distribution data: Global Avian Invasions Atlas (GAVIA; Dyer et al., 2017), Distribution of Alien Mammals (DAMA; Biancolini et al., 2021), and Global Naturalized Alien Flora (GloNAF; van Kleunen et al., 2015, 2019). The fourth database provided the year of the first record of a non-native species in the wild in a particular region (FirstRecords database; Seebens et al., 2017), and the fifth database (PREDICTS) provided information on the species composition of local assemblages under different LU regimes (Hudson et al., 2014, 2017). We hypothesized that the likelihood of occurrence of non-native species in local assemblages has a positive relationship with their regional residence time, with “region” defined as a larger mainland area such as a country, an island, or archipelago. We expected this relationship because a longer residence time in a region implies increased opportunities for propagules to reach and establish in more local assemblages within a region. However, as the spread of the species approaches distributional equilibrium, this relationship should level off. We also expected that the relationship between regional residence time and local occurrence varies among LU-types, as ecosystems used by humans might a priori be easier to colonize than (near-) natural ones. In human-used ecosystems, non-native species spread can be facilitated by reduced biotic resistance, environmental disturbance, and resource overabundance (Daly et al., 2023). Here, they might need lower propagule pressure—usually implicit to shorter residence times—for successful establishment, and they often also are spatially closer to foci of introduction. As a corollary, we expected that the likelihood of local occurrence of a non-native species should be proportional to regional residence time and that this relationship should level off earlier in human-used ecosystems than in undistributed ones. Finally, we also assumed that the correlation between regional residence time and local occurrence varies among plants, birds, and mammals because of their differences in generation length and dispersal ability, which influences their times to reach distributional equilibrium. In particular, plants are on average less mobile than birds and mammals, resulting in lower likelihood of local occurrence at any given residence time and a longer time required until the relationship with residence times levels off.

To test these hypotheses, we first used the regional-scale non-native distribution databases GAVIA, DAMA, and GLONAF to identify the non-native species in the local assemblage records of PREDICTS. Then, from the FirstRecords database, we obtained the first recorded date of observation of each non-native species present in PREDICTS within the region of the focal assemblages. We interpreted the times between the first record of a species in a region and the times at which the PREDICTS assemblages in this region had been sampled as waiting times or times-to-event. Put differently, we asked how the likelihood of finding a non-native species in a local assemblage is influenced by the time since its regional first record. We used the Kaplan–Meier estimator (Goel et al., 2010) and Cox proportional hazard models (Cox, 1972) to describe these waiting times and to analyze whether they differ among LU-types. In a complementary approach, we assigned each PREDICTS assemblage the mean residence time across all non-native species in the region, and then used regression models to analyze how the likelihood of finding at least one of these non-native species, as well as their proportional contribution to the species composition of local assemblage, depend on regional residence time, LU type and their interaction. The rationale behind is that the cumulative propagule pressure of the entire non-native species pool within a region should rise with its mean residence time. Consequently, the occurrence of at least one, or more, non-native species becomes more likely with longer residence times.

## 2 | MATERIALS AND METHODS

The data used in this study were collected by combining databases that report regional-scale distributions of non-native species, regional residence times of non-native species, as well as the full (native and non-native) species composition of local assemblages within the regions (see below for details). Although the taxonomic scope of available information would have been larger for each of the three aspects covered by these databases, their intersection delivered datasets sufficiently large for analysis in the case of mammals, birds, and vascular plants only.

Based on these data, we first analyzed the relationships between residence time and non-native occurrence in local assemblages at the species level. Second, we modeled the relationship between the mean or median residence time of all non-native species in a region (mean or median regional residence time) and the likelihood that at least one non-native species has colonized a local assemblage, and between this mean or median residence time and the proportional contributions these colonizers make to the entire species set of the assemblage. A flowchart illustrating the methodological steps is presented in Figure 1.

### 2.1 | Data collection

### 2.1.1 | Regional-scale distribution of non-native species

Information on the distribution of non-native species at the regional scale were taken from the GAVIA (birds; Dyer et al., 2017), DAMA (mammals; Biancolini et al., 2021), and GloNAF (vascular plants; van Kleunen et al., 2015, 2019) databases (Table S1). Additional distribution data were obtained for nine ubiquitous synanthropic mammal species not mapped in DAMA (*Bos taurus*, *Canis familiaris*, *Capra hircus*, *Equus asinus*, *Equus caballus*, *Felis catus*, *Mus musculus*, *Ovis aries*, and *Sus scrofa*) from various sources (Table S1). We overlaid non-native species distributions reported in these databases onto the common regionalization scheme of Biodiversity Information standards, formerly the Taxonomic Databases Working Group (TDWG level 4), which distinguishes 609 terrestrial regions (423 mainland regions and 186 islands or archipelagos; Brummitt, 2001). These regions are composed of high-level administrative areas, such as countries or states and provinces of larger countries (e.g., USA), while keeping islands separated even if they are part of the same administrative area. As a result, we obtained regional occurrence information for 361 non-native birds across 517 regions, 239

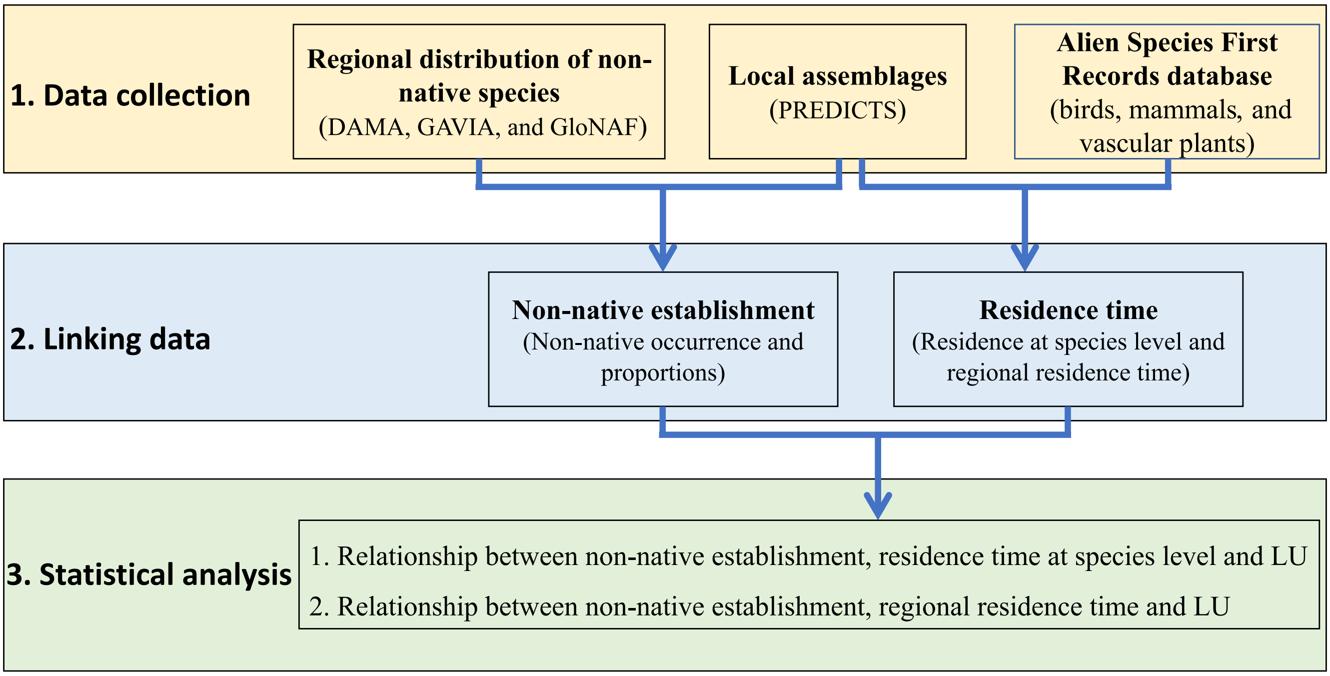

FIGURE 1 A flowchart illustrating the steps used in our study. There are three steps for (1) data collection, (2) linking data, and (3) statistical analysis.

non-native mammals across 219 regions, and 15,111 non-native vascular plants across 448 regions.

### 2.1.2 | Species composition of local assemblages

We obtained lists of species co-occurring in local assemblages within regions from PREDICTS (Hudson et al., 2014, 2017). This database holds a global collation of 666 individual studies that collectively report the species composition of 26,114 local assemblages under different kinds of LU; study site was recorded as a factor (SS); for studies with blocked designs, block with study was also recorded as a factor (SSB). Assemblages are defined as sets of species sampled by the authors of the original studies according to their specific sampling designs, most often plots or transects of varying size (between 0.06 and 39,150 m of linear extent, with a median value of 60 m). Sampling methods were consistent within each study site. During data compilation, the PREDICTS team had used information in the source publications to assign each assemblage to the LU-type that best describes the LU within the sampled perimeter or, if the maximum linear extent sampled is <10 m, the 100 $m^2$ centered around the sampled perimeter. They thereby distinguished six LU-types: Primary (natural habitat types not known to have ever been heavily altered by human actions), Secondary (various kinds of secondary successions after cessation of human use), Plantation (previously cleared areas planted with crop trees or crop shrubs), Pasture (regularly or permanently grazed by livestock), Cropland (land planted with herbaceous crops), and Urban (human habitation and/or buildings, including the surrounding gardens and green spaces). The vast majority of data was sampled between 1984 and 2013.

The studies compiled in PREDICTS document the species composition of local assemblages at different levels of taxonomic rank. While most contain complete species lists for larger taxonomic groups/ranks, some had a narrower focus on particular families, genera or even individual target species. To avoid bias in this analysis, we only included assemblages with full species lists at the same taxonomic rank as the databases of non-native species' regional distribution described above. However, to avoid losing assemblages nested within higher ranks in the PREDICTS collection, we also included studies referring to Animalia and Chordata. From the assemblages in the latter studies, we then selected the species lists of Mammalia and Aves. The status of the species in the assemblages, for example, whether it is breeding or not, is not consistently documented and could hence not be considered in the analysis. All assemblages finally included in this study were assigned to TDWG level 4 regions according to their geographical coordinates as reported in the original studies.

### 2.1.3 | Regional residence time

Information on the regional residence time of individual non-native species was taken from the latest version (version 2.0; https://doi.org/10.5281/zenodo.4632335) of the Alien Species First Records database (Seebens et al., 2017). This database collects the earliest year a non-native species was recorded in a region from >100 different sources including online databases, scientific peer-reviewed publications, reports, books, and personal collections. It currently includes 61,751 entries for 23,191 species (across taxonomic groups from all kingdoms) in regions that mostly match those of TDWG level 4. For birds, mammals, and vascular plants in our study, first records between 1500 and 2020 were available for 958, 255, and 11,043 non-native species, respectively.

## 2.2 | Linking databases

Before linking information from the different databases, all species names were standardized to the taxonomic backbone of the Catalogue of Life, a comprehensive database including *c*. 80% of all species known to science, by means of the *rcol* package in R (version 0.2.0, 2021; Banki et al., 2019).

Species in local assemblages were classified as non-native if they were listed in DAMA, GAVIA, or GloNAF for the region in which the assemblage is located. Based on this link, we calculated the occurrence of non-native species in each assemblage (= at least one native species is listed) as well as their proportion (the ratio of non-native species number to the total species number in the assemblage).

We calculated the species-specific residence time—at the time of sampling of the species in an assemblage—of each non-native species recorded in PREDICTS from the FirstRecords database (Seebens et al., 2017) as the time between the year the species has first been recorded in the focal region and the year of sampling of the local assemblage. To avoid bias by a few outliers with highly uncertain early first records in some regions, we limited our analysis to species with first records after 1800 AD Moreover, we excluded cases (i.e., combinations of a non-native species and an assemblage) where the non-native species had been first recorded (according to the FirstRecords database) more recently than the sampling time of local assemblage in PREDICTS. As the FirstRecords database does not consistently refer to TDWG level 4 regions (with 36, 22, and 26 regions for birds, mammals, and vascular plants, respectively), residence time at species level and mean (and median) residence times were computed for TDWG level 3 regions in case of USA, Brazil, and China (17, 15, and 14 regions correspondingly).

Mean and median regional residence times were computed for each local assemblage within the focal region as the difference between the mean or median year of first record of all species in the regional non-native species pool and the date an assemblage has been sampled. As in the case of species-specific calculations, species first recorded before 1800 AD and cases where the species' first recorded was later than the year of sampling of the assemblage were not considered (Table S2). Of the local assemblages compiled in PREDICTS, we could assign mean/median residence times to 4882, 933, and 4150 assemblages of birds, mammals, and vascular plants, situated in 58, 24, and 44 regions (i.e., countries, states, and provinces), respectively. A total of 568 assemblages (6% of the total) were excluded because they were located in regions without data from the FirstRecords database.

## 2.3 | Statistical analysis

### 2.3.1 | Relationships between non-native occurrence, residence time at species level, and land-use

To analyze how the likelihood of observing a non-native species in an assemblage changes with the residence time of this species, we used time-to-event analysis, also called survival analysis (*survival* package, version 3.5-7). Time-to-event analysis is a set of statistical methods tailored for analyzing how the waiting time until an event occurs depends on covariates (Therneau, 2023). This tool fits purpose as the time between a species' establishment in a region and its colonization of an assemblage can be considered an observed waiting time. The data matrix entering the model thus has, for each focal region, a number of rows equal to the number of assemblages within the region multiplied by the number of non-native species with first records in this region. For each row, "1" symbolizes that the species has been observed in the assemblage, indicating a colonization event has occurred within its regional residence time, or "0" if this was not the case. As each assemblage has only been surveyed in a single time period, the data are considered right-censored.

In a first step, we visualized these data by means of nonparametric Kaplan–Meier estimates with cumulative event transformation of the survival function, that is, of the waiting time until an assemblage gets colonized by a species, stratified by LU-type. Subsequently, we fitted a mixed-effects Cox model with LU-type as fixed-effects predictor using the package *coxme* in R (version 2.2-18.1; Therneau, 2022). We compared the following random effect structures for this model: (1) non-native species in the FirstRecords database, (2) regions in the FirstRecords database, and (3) non-native species and regions (combined together). The best model was selected based on the lowest Akaike information criterion (AIC). For the fixed factor LU-type, "Primary" was considered as the reference level. Since the number of local assemblages in LU-types other than Primary and Secondary was low (Table S3), we grouped Plantation and Pasture into a single "Plantation-Pasture" category, because both consisted mainly of perennial vegetation. Additionally, we combined local assemblages in Cropland and Urban areas into one single "Cropland-Urban" category as they are subjected to similar and strong anthropogenic impact. The factor LU-type thus had four levels (Primary, Secondary, Plantation-Pasture, and Cropland-Urban) in our models. We fitted these mixed-effects Cox models both for each taxonomic group separately and across all three taxonomic groups. In the case of mammals, we could not include assemblages in the Cropland-Urban category because their number was too low (only one assemblage). Cumulative event curves were visualized by the ggsurvplot function in *survminer* package (version 0.4.9.999; Kassambara et al., 2021).

### 2.3.2 | Relationships between non-native occurrence, regional residence time, and LU

We applied logistic mixed-effects regression models to test whether the occurrence of at least one non-native species (binary response: 0–1) in an assemblage depends on the mean or median residence time of the regional non-native species pool and the type of LU. Given our hypothesis that LU-types differ in the rates at which local assemblages are colonized by non-native species, we included an interaction term of these two predictors into the model (full model: non-native occurrence~residence time × LU-type). We used the *glmer* function from the *lme4* package (version 1.1-32) with a binomial error distribution (Bates et al., 2015). The model was initially fitted with random intercepts for study-site blocks (SSB) nested within study sites (SS) and taxa (SSB/SS/taxa). Mean and median residence time were included in alternative models. In addition to the full model, we also fitted models without an interaction term (subset model: non-native occurrence ~ residence time + LU-type), with random-effect terms as in the full model. We used AIC and likelihood-ratio tests (LRTs; Liu et al., 2023) to select the simpler model if the more complex one did not differ in AIC by more than two points, and the *p*-value of the LRT comparing the two models was <.05. Based on the selected model, we predicted non-native occurrences in response to residence time, together with their 95% confidence intervals, for the LU-types by means of *ggeffects* (version 1.2.0) with marginal effects of model terms (Lüdecke, 2018). We applied the analytical procedure described both on the entire dataset (including all three taxonomic groups and SSB/SS/taxa as the random effect) and for each taxon (SSB/SS as the random effect) separately.

As logistic mixed models are inflexible in the functional relationship between response and predictor variables, we additionally used generalized additive mixed models (GAMMs) to explore signs of saturation in the relation between non-native occurrence and residence time. We refitted the models of non-native occurrence described above using the gamm4 function of the R-package gamm4 (version 0.2-6; Wood & Scheipl, 2022), incorporating a spline smoother on the predictor residence time. We then visually inspected the predictions from this GAMM to determine whether the slope of the fitted regression lines level off at particular residence times, both across taxa and for the individual taxonomic groups.

### 2.3.3 | Relationships between non-native proportions, mean regional residence time, and the LU-types

We analyzed the dependence of the proportion of non-native species in an assemblage on residence time and land-use by generalized linear mixed-effects models with Template Model Builder from the *glmmTMB* package (version 1.1.6), employing a beta error distribution as recommended for data with lower and upper bounds such as proportions (Brooks et al., 2022). Only assemblages with at least one non-native species were included in this analysis. As in the case of the occurrence model, we used random intercepts for study-site blocks (SSB) nested in studies (SS) and taxa (SSB/SS/taxa as random factor) across all taxa and for each taxon (SSB/SS as random factor) separately. In our data, non-native proportion in some assemblages was 1, that is, all species within these assemblages were non-native. Given that the beta distribution does not include the value 1, we applied a lemon-squeezer transformation to the response variable before fitting the model (Smithson & Verkuilen, 2006). Further analytical steps were the same as for non-native occurrence, that is, we fitted full models with an interaction term and reduced models without an interaction term for both the full dataset and each taxon separately. We compared full and reduced models using AIC and LRT.

### 2.3.4 | Sensitivity analysis

We performed sensitivity tests to assess the model's response to variation in spatial coverage of local assemblages among different biomes in PREDICTS. We allocated the geographical location of each assemblage to one of the 14 biomes (Olson et al., 2001). We performed a leave-one-out cross-validation that fitted the same models for regression coefficients, non-native occurrence and proportions described above but excluding the assemblages from one biome in turn (Liu et al., 2023; Newbold et al., 2015). We subsequently calculated the means of all model coefficients, standard errors, and the 95% confidence intervals.

In addition, we tried to include several additional variables into the model to test for the robustness of our findings to alternative model formulations. We first added the number of non-native species in a region to the fixed-effect predictors in the models relating non-native occurrence and proportions to mean regional residence time, based on the rationale that a larger set of species might lead to a more rapid colonization of local assemblages by at least one species. Second, we included the area of a TWDG region as an additional fixed-effects predictor into the models. A larger area might imply more dispersed assemblages, requiring a species to be present for longer to successfully colonize, thereby influencing the relationship between residence time and non-native occurrence and proportion. Both the number of non-native species and area of the region were log-transformed to reduce skewness of the data. We evaluated whether these additional variables affect the parameter estimates calculated for residence time, LU-type, and their interaction in the original model. Third, we tested the models by adding the TDWG level 4 region in which an assemblage is located as an additional random factor (SSB/SS/taxa/region) in the models across all taxa and for each taxon (SSB/SS/region) to account for possible region-specific variation in the relationship between residence time and non-native occurrence and proportion.

All analyses were performed in R version 4.2.3 (R Core Team, 2023) and the figures were created using the ggplot2 package (version 3.4.1; Wickham, 2011).

## 3 | RESULTS

### 3.1 | Distribution of local assemblages with non-native species and residence time

The assemblages were not evenly distributed across the globe, with large gaps in northern Asia as well as parts of Africa and central and western North America (Figure 2a; Figure S1). The mean time between the first record of a non-native species within a region and its sampling date in a PREDICTS assemblage was 121 years, with shorter values for birds (63 years) than for mammals (94 years) and vascular plants (97 years). For assemblages containing at least one non-native species, the contribution of these non-natives to the complete list of species per assemblage was 28% on average (Figure 2b). This contribution was particularly high in mammals (70%) because half of these assemblages (142 out of 293) consisted exclusively of non-native mammals in Australia, Canada, and Argentina; the contributions were much lower in birds and vascular plants (18% and 21%, respectively; Figure 2c–e).

### 3.2 | Effects of LU-type on time until non-native colonization based on species-specific residence times

The cumulative event curves indicate clear differences in the times until a non-native species colonizes assemblages of different LU-types in a focal region for birds and vascular plants (Figure 3b,d). For birds, the time until half of the assemblages in Cropland-Urban are colonized was estimated as 75.5 years, in Plantation-Pasture 168 years, and in Secondary and Primary >205 years. For vascular plants, the respective values were 85 years in Cropland-Urban, 134 years in Secondary, and ca. 200 years in Plantation-Pasture and Primary. For plants, the curves also showed a more or less linear increase in the likelihood of finding a non-native species in an assemblage with time in the types of Cropland-Urban and Secondary Vegetation. In contrast, the likelihood of finding a non-native species remained low for >100 years and then started to increase faster in the case of Plantation-Pasture and Primary. For mammals (Figure 3c), the curves were very similar across all LU-types (but note that assemblages from Cropland-Urban were not included in this model). With all species combined (Figure 3a), the results were similar to those observed for the vascular plants alone, due to this group's dominance in the dataset.

The best-fitting mixed-effects Cox models with a random effect for non-native species identity and region combined were largely in line with cumulative event estimates (Table S4), but differed in some respects (Figure 4a–d; Table S5). First, owing to the large sample size, all LU-types had significantly different times until non-native

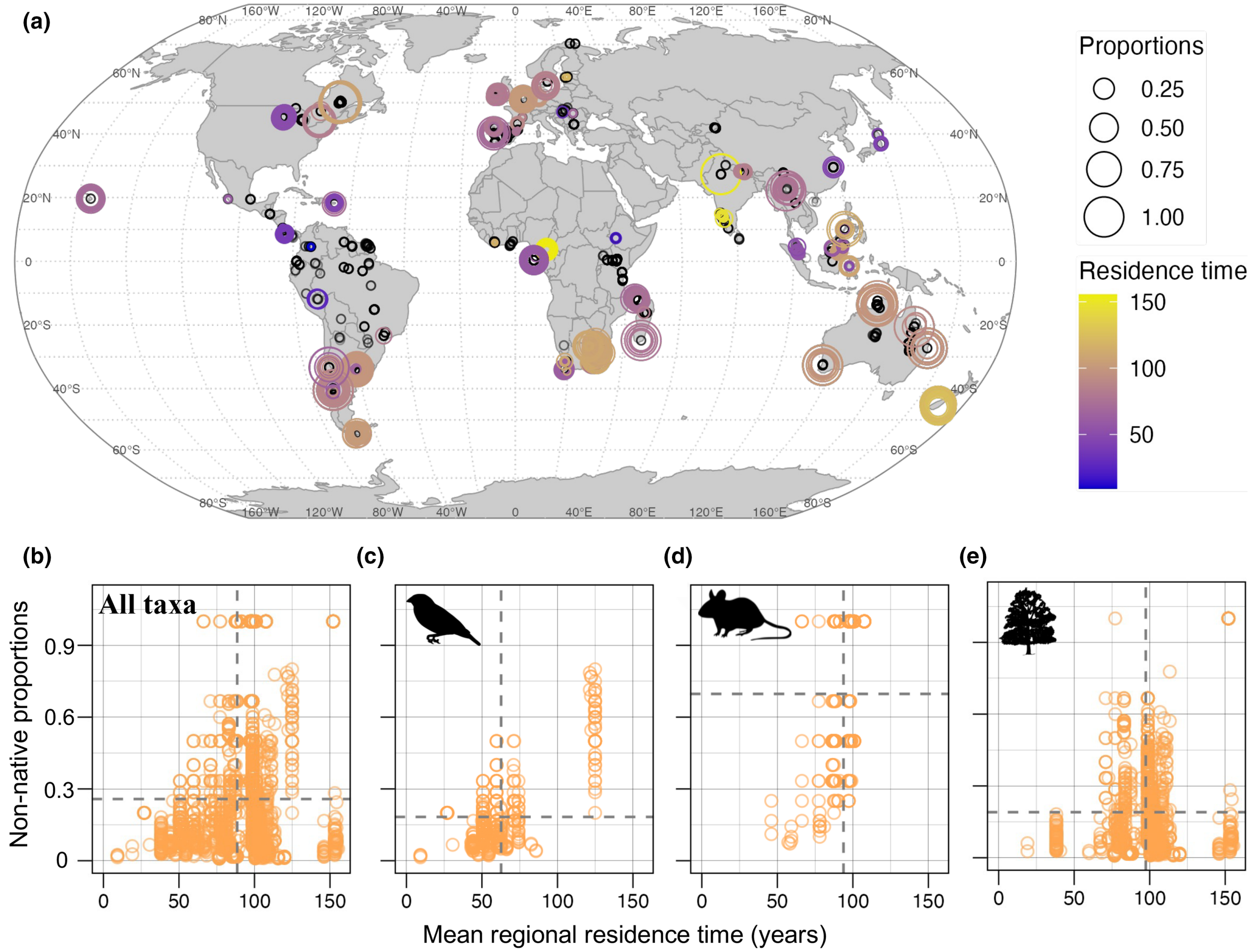

FIGURE 2 Geographic distribution of local assemblages, the proportions of non-native species in these assemblages, and mean regional residence times of non-native species. In (a) colored circles represent assemblages that contain at least one non-native species, and black circles represent assemblages containing no non-native species. Colors symbolize the mean regional residence times of species, calculated as the difference between the average year of the first record of all non-native species in the TDWG region and the year the assemblage has been sampled. Circle sizes represent the proportions of non-native species among all species in the assemblages. The scatterplots (b–e) only show assemblages containing at least one non-native species and depict the relationship between the proportion of non-native species among all species in the assemblage as a function of the mean residence time of all non-native species in the region across all taxa (b), and separately for birds (c), mammals (d), and vascular plants (e). The gray dashed lines represent the mean values of regional residence time and non-native proportions, respectively. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

colonization compared to the reference levels of Primary, even if differences in these times were numerically small as in the case of mammals. Second, the rankings of colonization times in birds (Cropland-Urban < Plantation-Pasture < Primary < Secondary; Figure 4b), mammals (Secondary < Primary < Plantation-Pasture; Figure 4c), and vascular plants (Cropland-Urban < Secondary < Plantation-Pasture < Primary; Figure 4d) were consistent between KM estimates and the Cox model. However, rankings differed slightly in the cross-taxon model where Secondary and Plantation-Pasture switched places (Cropland-Urban < Plantation-Pasture < Secondary < Primary; Figure 4a). We found that results from the sensitivity analysis with respect to spatial biases from uneven sampling across biomes did not change the patterns of regression coefficients delivered by the Cox model (Figure S2; Table S6).

## 3.3 | Relationship between mean regional residence time, LU-type and non-native occurrence

Based on the AIC and LRTs, a model including mean regional residence time and LU-type as predictors (without their interaction) was identified as the best fit for explaining non-native occurrence across taxa (Table S7). The results of models using median instead of mean residence times were very similar. As expected, the probability of finding at least one non-native species in an assemblage increased with the mean residence time of the non-native species of a region in each LU-type (Figure 5a; Table S8), with low probabilities up to a residence time of ~50 years and an increase to values >50% in all LU-types after 150 years. The relationship between non-native occurrence and residence time did not differ significantly

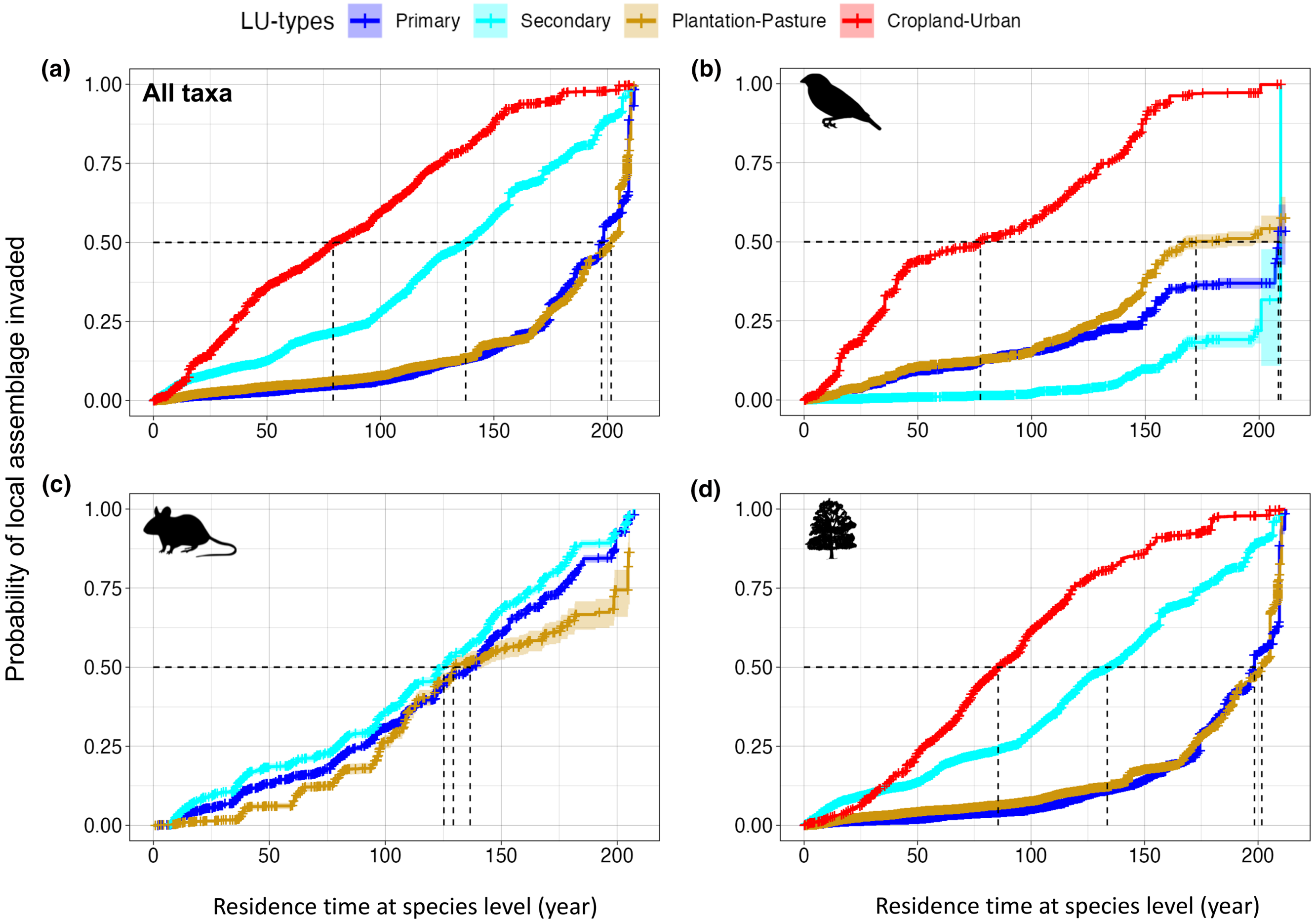

FIGURE 3 The probability of local assemblages invaded in relationship with species-specific residence time. Probabilities are analyzed using the Kaplan–Meier estimate with cumulative event transformation across all taxa (a), and separately for birds (b), mammals (c), and vascular plants (d). The shaded areas represent 95% confidence intervals; the colors distinguish LU-types. In the case of mammals, LU-type Cropland-Urban was not included in the model due to small sample size. Dashed lines indicate the residence time that is needed for 50% of local assemblages that were invaded among different LU-types.

between Primary and other LU-types. However, and in accordance with the species-level analyses, predictions of the model clearly indicate a later onset of assemblage colonization in Primary, with a delay of several decades as compared to Cropland and Urban areas (Figure 5a).

For the individual taxonomic groups, full models with an interaction term between residence time and LU-type fit the data best in the case of birds and vascular plants, but not in the case of mammals (Figure 5b–d; Table S7). The relationship between residence time and non-native occurrence was most strikingly different among LU-types for birds (Figure 5b; Table S8), and even after 120 years the estimated probability of finding a non-native bird was still almost zero in Primary, but >75% in Cropland and Urban areas (Figure 5b). For vascular plants, non-native species appeared in Cropland and Urban areas as well as in Plantation and Pasture after mean residence times <20 years, and their occurrence increased almost linearly with longer residence times. In contrast, for Primary, the likelihood of finding a non-native plant species started to rise only after approximately 75 years of mean residence time but increased rapidly thereafter (Figure 5d; Table S8), echoing the results of the KM curves based on individual species residence times (Figure 3d). For mammals, the relationship between residence time and non-native occurrence did not differ significantly among LU-types (Figure 5c). However, the LU-type with the earliest onset of non-native occurrence in the other two groups, Cropland and Urban, was not included in the model for mammals due to the small sample size.

Sensitivity analyses (see Section 2 for details) suggested that the results were robust to geographical bias in the assemblage data (Figure S3). Adding non-native species richness of a region as an additional predictor to the model turned residence time statistically nonsignificant in the case of mammals; however, it did not qualitatively affect the results for models of birds, plants, and across all three groups (Table S9). Adding the size of the individual regions as an alternative predictor improved the fit of the model across all taxonomic groups, but it did not change the relationship with residence time (Tables S10 and S11). Furthermore, adding regional identity as an additional random term to the models did not improve the models, except the model across all taxa (Table S12).

The GAMM with a spline smoother on residence time did not indicate a deceleration in non-native occurrence within the range of

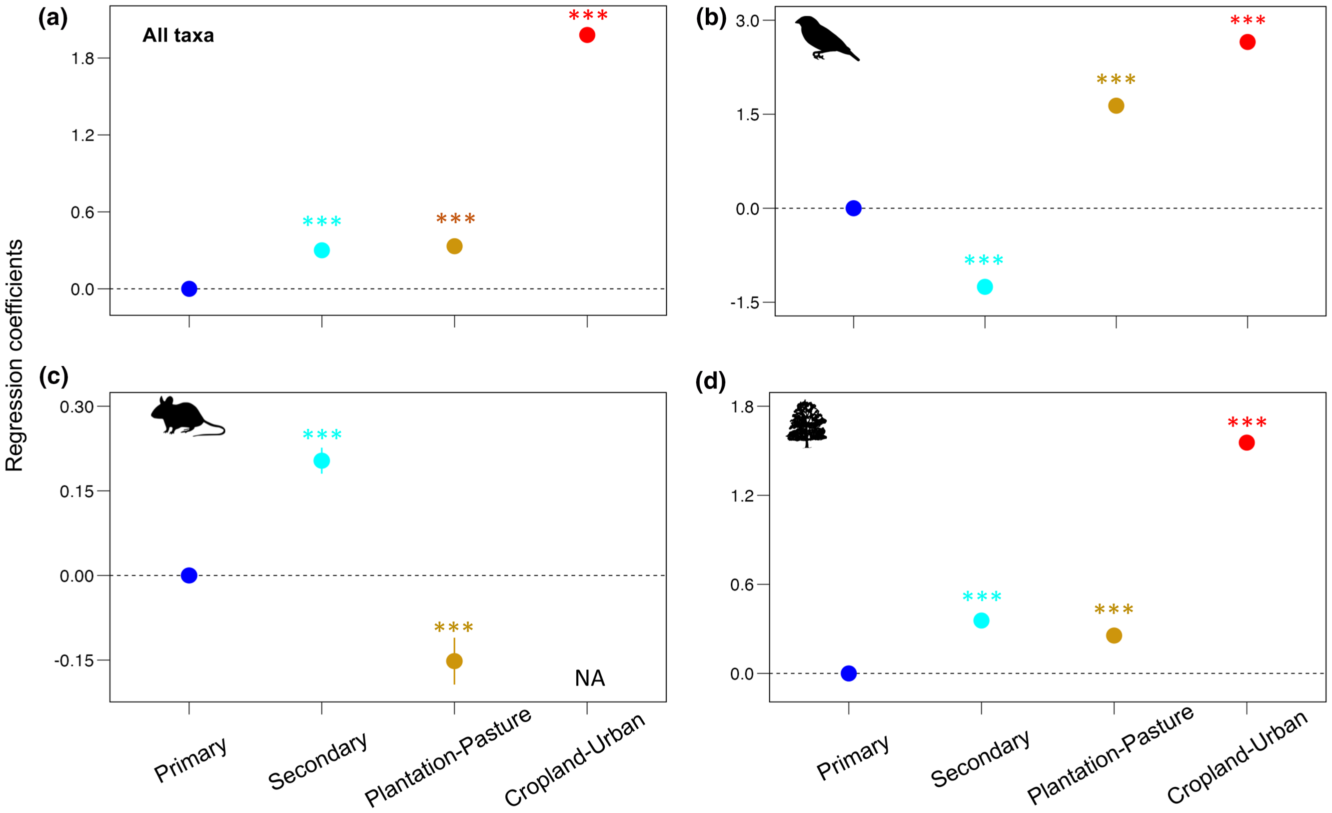

FIGURE 4 Regression coefficients of residence time required compared to the reference levels of Primary. Mixed-effects Cox regression models were analyzed across all taxa (a), and individually for birds (b), mammals (c), and vascular plants (d). In the case of mammals, LU-type Cropland-Urban was not included in the model due to small sample size. The coefficients and standard errors compared to Primary (reference level) are shown and the asterisks indicate significant deviations from the reference level ($p$-values: $^{***}p < .001$). Positive coefficients indicate that the colonization local assemblages was faster (shorter residence time) than in Primary (as reference). Negative coefficients indicate that colonization took longer than in Primary.

residence times covered by the data, for most combinations of taxa and LU-types (Figure S4). In the cross-taxon model, the rise of non-native occurrence probability apparently leveled off after approximately 150 years for almost all LU-types except Primary.

## 3.4 | Relationship between mean regional residence time, LU-type and non-native species proportions

Across taxonomic groups, and for mammals and vascular plants individually, the most parsimonious models for explaining the proportion of non-native species in local assemblages included residence time and LU-type, but not their interaction (Table S7). For birds, the relationship between residence time and non-native species proportions differed between LU-types. Across taxa, these proportions increased from ca. 10% to 50% between 20 and 150 years of mean residence time (Figure 6a). The increase with residence time was particularly strong in mammals which reached high proportions after about 100 years (Figure 6c). For birds (Figure 5b) and vascular plants (Figure 6d), the models also indicated a rise in non-native proportions with residence time, although the levels remain much lower until the longest mean residence times recorded. However, the regression coefficients were not significantly different from zero in the separate models of these two taxonomic groups (Table S13). For birds, the non-significant main effect of residence time is due to a consistently low proportion of non-native birds in Primary, while the proportions rise with residence time in the other LU-types. In the case of vascular plants, the rise of non-native proportions was apparently slow in all LU-types. The reported results were robust with respect to (1) biases in the distribution of assemblages across biomes (Figure S5) and (2) the inclusion of regional identity into the random-effects structure (Table S12). They also did not change when adding the number of non-native species in a region (Table S9) or region area as an additional fixed-effects predictor to the models (Tables S10 and S11).

## 4 | DISCUSSION

The two complementary approaches used here consistently demonstrate that the encroachment of non-native species into local assemblages is a process that takes decades to centuries, on average, in all

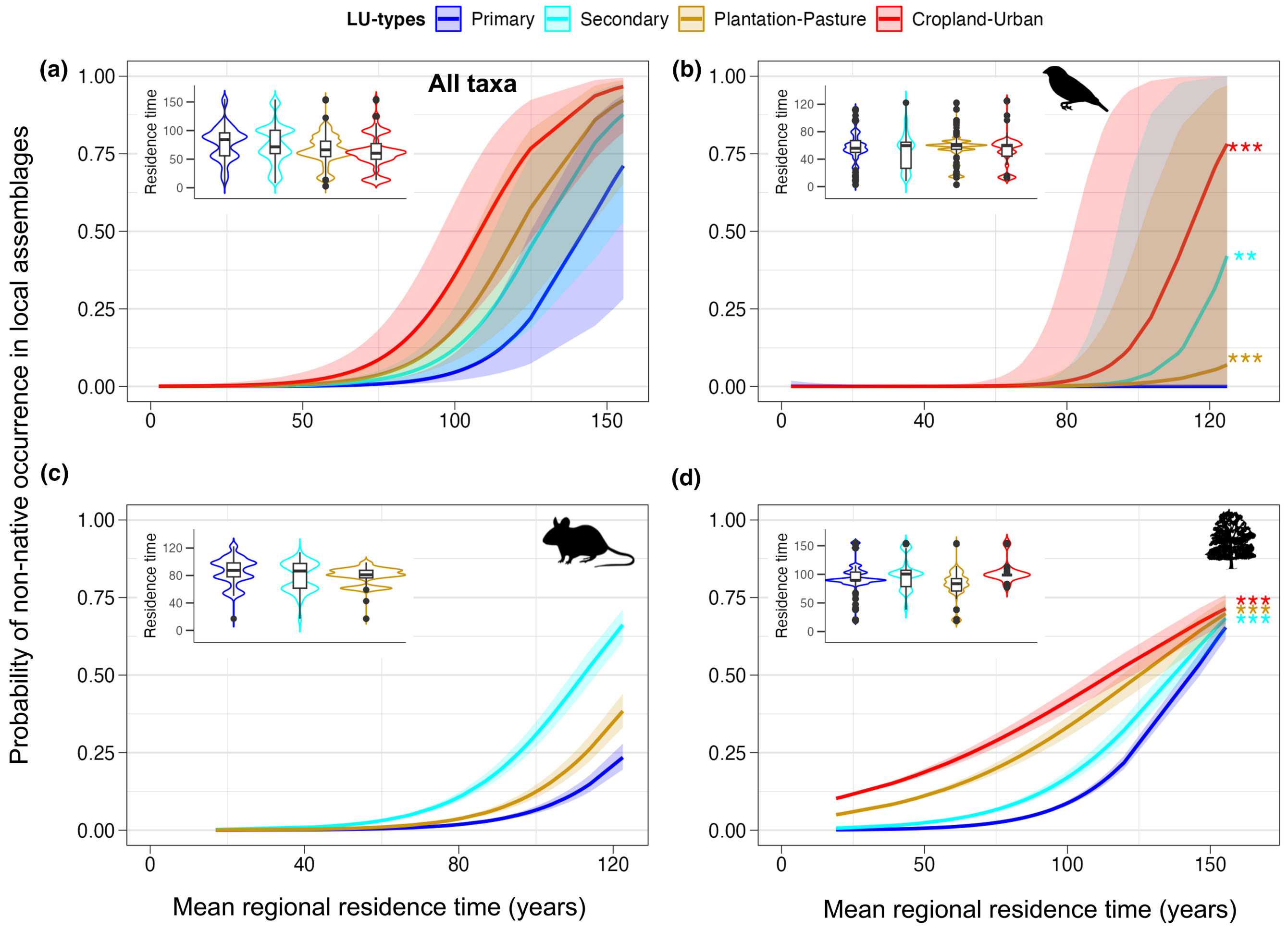

FIGURE 5 Probability of finding at least one non-native species in a local assemblage as a function of mean residence time of all non-native species in a region. Probabilities are predictions from generalized linear mixed-effects models fitted across all taxa (a), and individually for birds (b), mammals (c), and vascular plants (d). Shaded areas represent 95% confidence intervals; colors distinguish LU-types. In the case of mammals, the LU-type, Cropland-Urban was not included in the model due to small sample size. Asterisks indicate significant differences from Primary (*p*-values: **<.01 and ***<.001). The inset violin plots show the differences in residence time among the LU-types.

the three taxonomic groups analyzed. With respect to non-native occurrence, both approaches agree in suggesting that the pace of encroachment varies among LU-types, in particular in the case of birds and plants. Non-native species tend to appear earlier in assemblages under a particularly strong human usage, namely Cropland and Urban. Consistent with our hypothesis, Primary was the LU-type with the slowest colonization rates in the case of plants. For birds and mammals, the results were less conclusive, but at least in case of birds, Primary becomes colonized much later than the two LU-types under most intense usage, Cropland-Urban and Plantation-Pasture. Both with respect to occurrence and (to a greater degree) non-native proportions, our results indicate that the integration of non-native species into local communities is still an ongoing process across all LU-types, particularly in Primary. Thus, if further influx of non-native species to a region would be haltered, this may lead, after a sufficiently long time, to a reduction of currently observed differences of invasion between natural and used ecosystems (Liu et al., 2023). However, if the influx continues, or even accelerates (Seebens et al., 2021), these differences may persist and deepen in the decades to come.

Interestingly, the proportion of non-native species in an assemblage did not increase significantly with residence time neither for birds nor for vascular plants. The reasons for this difference cannot be identified with correlative models. However, we suggest that several factors might contribute to this finding. First, colonization of local assemblages by one non-native species takes less time than colonization by multiple species. The time span covered by the gradient of mean residence times in our data might thus be too short to detect the effect of residence times on non-native proportions. Second, non-native proportions are under the control of additional sources of variation, such as native species richness or competition between already present and newly colonizing non-natives (Alexander & Levine, 2019; Gioria et al., 2023). Third, the ongoing turnover in local species composition, mostly in response to LU change, implies a progressive replacement of specialist species by generalists, including non-natives (Newbold et al., 2018; Xu et al., 2023). As this process is itself accelerating

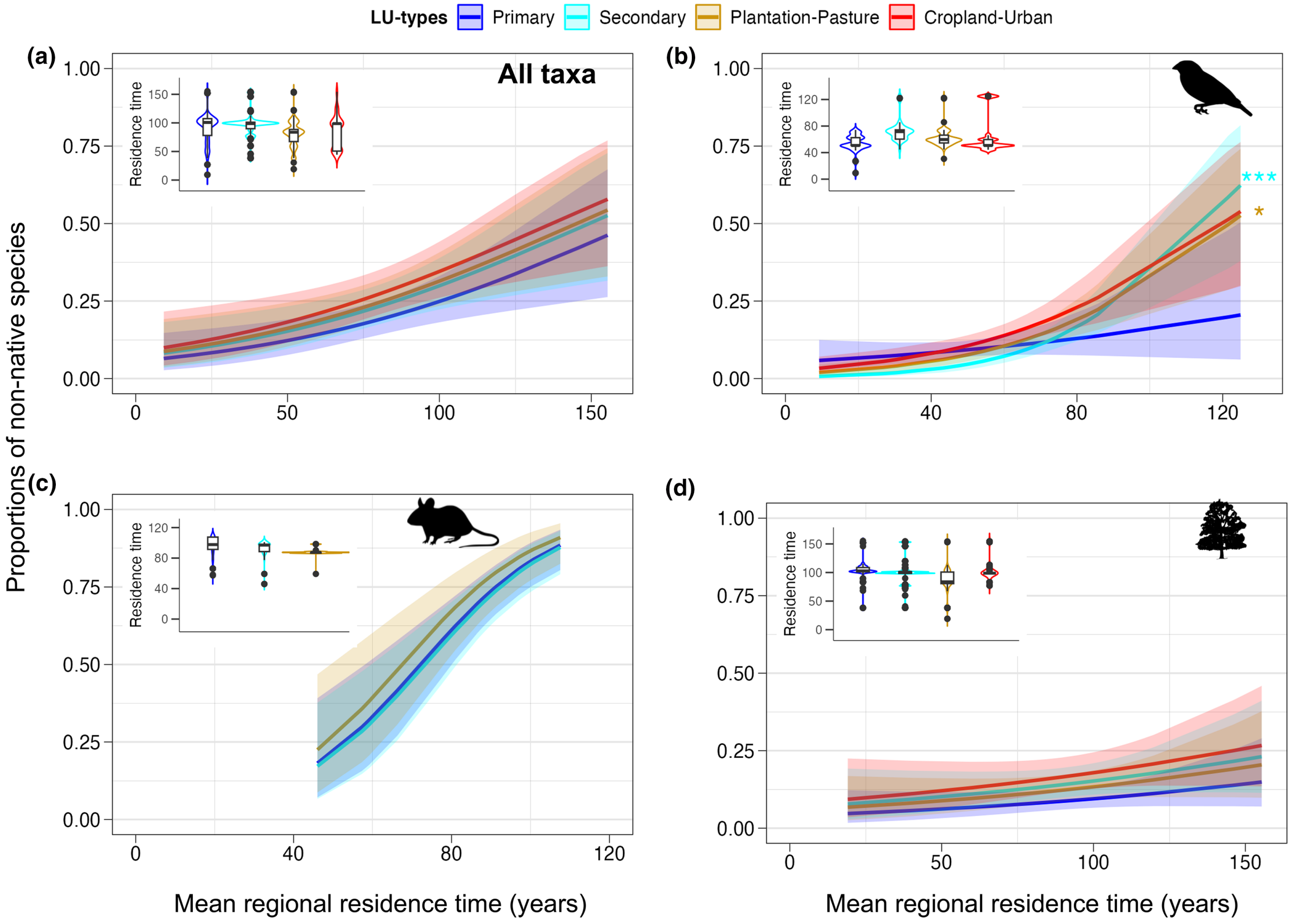

**FIGURE 6** Proportion of non-native species among all species in local assemblages as a function of the mean residence time of all species in a region. Proportions are predictions of generalized linear mixed-effects models fitted across all taxa (a) or for birds (b), mammals (c) and vascular plants (d) separately. Shaded areas represent 95% confidence intervals, the colors distinguish LU-types. In the case of mammals, the LU-type Cropland-Urban was not included in the model due to small sample size. Asterisks indicate significant differences from Primary (*p*-values: *<.05 and ***<.001). The inset violin plots show the differences in residence time among the LU-types.

over the most recent decades at different rates in different regions (Newbold et al., 2018), it may distort the relationship between residence time and the proportion of non-native species.

## 4.1 | Differences among LU-types

We found significant variation in the relationship between residence time (both at species level and regional level) and non-native species occurrence across different LU-types. Cropland and Urban areas become colonized earlier and quicker than other LU-types, probably because Urban areas are introduction hubs (Aronson et al., 2014) and human disturbance is high in both LU-types, a factor known to favor non-native species (Chytrý, Jarošík, et al., 2008; Liu et al., 2023). In contrast, predictions of our models suggest that the probability of finding a non-native species in Primary starts to rise with a delay of several decades (and up to a century) in comparison to Cropland and Urban. Both a higher biotic resistance, lower disturbance and longer distances from introduction hotspots likely contribute to the slower rates of encroachment in near-natural ecosystems compared to other LU-types. However, at least for plants, the data also suggest that after this longer time lag, the colonization of Primary might accelerate considerably, so that differences in the likelihood of non-natives occurrence between LU-types decreases with increasing residence time (Figure 5d). Differences in the occurrence of non-native species in Primary compared to other LU-types appear thus partly due to slower colonization rates and hence longer pay off times of the invasion debt, particularly in vascular plants (Liu et al., 2023). For birds, the cumulative event curves suggest a similarly long time until non-native colonization starts to become more frequent, not only in Primary but also in Secondary and in Plantation and Pasture, and with a less pronounced acceleration after long residence times. The models based on species-specific residence times and those based on mean residence times are also not completely consistent in the case of non-native bird occurrence, but agree in showing relatively fast colonization of Cropland and Urban areas and slow colonization of Primary. The particularly late colonization of Primary may, again, indicate lower colonization pressure (Dyer et al., 2016, 2017), but also stronger competition from native bird communities. For mammals, the models for both the non-native occurrence and proportions did not show the differences between the LU-types, which may be attributed to the insufficient data, especially in Cropland and Urban areas. However, various studies have shown that mammals are often introduced in natural and near-natural environments, thus decreasing their difference in these intensively used ecosystems (Clout & Russell, 2008; Latham et al., 2017; Tedeschi et al., 2022).

In contrast to non-native occurrences, the increase of non-native proportions with residence time did not differ across LU-types except for birds. In addition to the reasons for this discrepancy discussed above, we note that proportions were analyzed only for the subset of assemblages which contained at least one non-native species. This selection introduces a bias against assemblages that are the most remote or most difficult to invade assemblages. As the latter are probably most frequent in Primary, the lack of LU-effects on the accumulation of non-native proportions may in part also result from this subset selection.

## 4.2 | Saturation

The gradient of mean residence times covered by our data spans between 120 (mammals and birds) and 150 years (vascular plants). At the end of this interval, our models, both GLMMs and GAMMs, predicted that the occurrence of non-native species in local assemblages was still increasing for most combinations of taxonomic groups and LU-types. Similarly, the sudden drop of Kaplan–Meier curves for all but Cropland-Urban in the case of birds, and for Primary and Plantation-Pasture in the case of plants, suggests that many species in these taxonomic groups need more than 150 years to colonize all suitable assemblages within a region. These findings suggest that the colonization of local assemblages will likely continue in many regions, even if strict regulations prevented new introductions to these regions. This is particularly true in the case of birds and plants in Primary, where all models indicate that occurrence starts to increase; late signs of saturation are missing in the mean residence-time models. The apparently long pay off times fit well with the considerable long-term invasion debt suggested by earlier studies (Essl et al., 2011; Williamson et al., 2009). For non-native proportions, conclusions are more difficult to draw. In the case of mammals, model predictions suggest a saturation at high values beyond 70% after about 100 years of mean residence time. However, both the higher speed and the higher absolute values reached might not be globally representative because nearly half of the samples used for analysis of proportions in mammals (140 out of 292) come from Australia. For the other two groups, the lack of a significant effect of residence time in the models of proportions might, as discussed, be due to even longer lag-times and other reasons, but these inferences remain speculative.

## 4.3 | Caveats

All five databases combined in this analysis come with a number of geographical biases, which are discussed in the respective publications that first introduced or used these databases (Biancolini et al., 2021; Hudson et al., 2014, 2017). For instance, the spatial coverage is mostly concentrated in intensively sampled temperate regions, such as Europe, North America, and Australia, and less exhaustive over large areas of Asia and the tropics, subject to lower effort and/or linguistic barriers. Coverage is also unequal across taxonomic groups with plants better represented than birds and mammals. In addition, the FirstRecords database (Seebens et al., 2017) provides information only on subsets of non-native species in individual regions. Further, first-record dates might represent the real onset of species naturalization unequally across regions and species, and precise colonization times of assemblages are unknown. This is because of time lags between the first record and the actual establishment and between the recording of the assemblage and the species' colonization. However, the times between the first record of a species in a region and the times when all the assemblages in this region (documented in PREDICTS) have been sampled, both those with and without the focal species, provides an estimate of the distribution of these waiting times. All these inaccuracies likely introduce considerable noise to the data (Liu et al., 2023). Nevertheless, our sensitivity analyses suggest that our results are robust against spatial sampling biases and that the sensitivity to the inclusion of additional predictors into the models is limited. Hence it is likely that better (i.e., more evenly distributed) sampling, and more accurate information on residence and colonization times, would reinforce the patterns detected rather than change them qualitatively.

# 5 | CONCLUSIONS

Taken together, our data suggest that most non-native species likely need decades or even centuries from their first detection in a region until they realize their potential distribution across local assemblages. The exchange of biota at the global scale thus takes considerable time to trickle down to the local scale. Given that most non-native species naturalizations are relatively recent (Seebens et al., 2017) and that their rate will probably continue to rise in the decades to come (Seebens et al., 2021), local assemblages will likely accumulate non-native species over the entire 21st century and beyond, contributing to the biotic homogenization of global ecosystems (Daru et al., 2021; Jandt et al., 2022; Yang et al., 2021). In natural and near natural ecosystems, which are of particular conservation concern, the consequences of current regional introductions for the future of local assemblages seem to unfold with particularly long lag times. This finding has implications for conservation as it suggests that the apparent resistance of these ecosystems of particular conservation concern against non-native colonization may eventually fade. Thus, whenever non-native species have the potential to threaten native diversity or ecosystem functioning, measures to combat their regional spread are hence sensible even if they currently appear confined to anthropogenic ecosystems and have not yet encroached into natural or near-natural ones.

The large temporal distance between cause and effect also makes the long-term consequences of non-native species introduction increasingly unpredictable, especially given many dynamic factors are involved in biological invasion other besides LU, for example, climate change, economic trade, wavering pathways of introduction, etc. The enforcement of national or regional legislation to restrict the import, transport, possession, and trades of non-native species (Essl et al., 2020) could function as an invasion-debt brake and reduce the negative impacts that current introductions impose on ecosystems and societies of the future.

## AUTHOR CONTRIBUTIONS

**César Capinha:** Data curation; writing–review and editing; **Daijun Liu:** Conceptualization; formal analysis; validation; visualization; writing – original draft; writing – review and editing. **Franz Essl:** Supervision; visualization; writing – review and editing. **Bernd Lenzner:** Conceptualization; formal analysis; supervision; validation; writing – review and editing. **Dietmar Moser:** Conceptualization; investigation; supervision; validation; visualization; writing – review and editing. **Philipp Semenchuk:** Validation; visualization; writing – review and editing. **Tim M. Blackburn:** Data curation; writing – review and editing. **Phillip Cassey:** Data curation; writing – review and editing. **Dino Biancolini:** Data curation; writing – review and editing. **Wayne Dawson:** Data curation; writing – review and editing. **Ellie E. Dyer:** Data curation; writing – review and editing. **Benoit Guénard:** Data curation; writing – review and editing. **Evan P. Economo:** Data curation; writing – review and editing. **Holger Kreft:** Data curation; writing – review and editing. **Jan Pergl:** Data curation; writing – review and editing. **Petr Pyšek:** Data curation; writing – review and editing. **Mark van Kleunen:** Data curation; writing – review and editing. **Carlo Rondinini:** Data curation; writing – review and editing. **Hanno Seebens:** Data curation; writing – review and editing. **Patrick Weigelt:** Data curation; visualization; writing – review and editing. **Marten Winter:** Data curation; writing – review and editing. **Andy Purvis:** Data curation; writing – review and editing. **Stefan Dullinger:** Data curation; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Bird distribution data was sourced from the Global Alien Invasions Atlas (GAVIA) database at https://figshare.com/articles/dataset/Data_from_The_Global_Avian_Invasions_Atlas_A_database_of_alien_bird_distributions_worldwide/4234850, mammal from DAMA at https://figshare.com/articles/dataset/DAMA_the_global_Distribution_of_Alien_Mammals_database/13014368, and vascular plants from Global Naturalized Alien Flora (GloNAF) Database at https://glonaf.org. The first record of a non-native species in the wild in a particular region can be found at https://zenodo.org/records/3690748. Local biodiversity measures were sourced from the Natural History Museum PREDICTS database at https://data.nhm.ac.uk/dataset/release-of-data-added-to-the-predicts-database-november-2022. The data and code for the analysis can be found in zenodo (https://zenodo.org/records/12672921).

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