

Secondary foundation species enhance biodiversity

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It has long been recognized that primary foundation species (FS), such as trees and seagrasses, enhance biodiversity. Among the species facilitated are secondary FS, including mistletoes and epiphytes. Case studies have demonstrated that secondary FS can further modify habitat-associated organisms ('inhabitants'), but their net effects remain unknown. Here we assess how inhabitants, globally, are affected by secondary FS. We extracted and calculated 2,187 abundance and 397 richness Hedges' *g* effect sizes from 91 and 50 publications, respectively. A weighted meta-analysis revealed that secondary FS significantly enhanced the abundance and richness of inhabitants compared to the primary FS alone. This indirect facilitation arising through sequential habitat formation was consistent across environmental and experimental conditions. Complementary unweighted analyses on log response ratios revealed that the magnitude of these effects was similar to the global average strength of direct facilitation from primary foundation species and greater than the average strength of trophic cascades, a widely recognized type of indirect facilitation arising through sequential consumption. The finding that secondary FS enhance the abundance and richness of inhabitants has important implications for understanding the mechanisms that regulate biodiversity. Integrating secondary FS into conservation practice will improve our ability to protect biodiversity and ecosystem function.

Primary foundation species (FS) (Fig. 1), such as trees, freshwater plants, salt marshes and seagrass, provide the initial physical framework for other species to inhabit, ameliorate environmental and biological stressors, and play an important role in determining patterns of biodiversity^{1–5}. Due to their critical role in modifying biodiversity, primary FS define many ecosystems and are often the targets of biodiversity assessments, conservation measures and restoration efforts^{4,6}. However, primary FS also provide habitat to secondary, dependent FS^{7–9} such as algal epiphytes and mistletoes attached to aquatic plants and trees, seaweeds entangled around seagrass leaves, or mussels embedded among marsh grasses^{8,10,11} (Fig. 1). Some secondary FS have obligate associations with the primary FS¹², while others can also persist on their own as primary FS themselves¹³ and thereby form facultative relationships with primary FS. Secondary FS are distinguished from other inhabitant species on the basis that they also provide structurally complex biogenic habitats that alters environmental conditions within the matrix of the primary FS.

Although secondary FS add habitat structure, they could have either a net negative effect or a net positive effect on inhabitants. Net negative effects might arise where secondary FS act as parasites or competitors of the primary FS, and thereby reduce the quality, quantity or stability of the habitat provided to inhabitants by the primary FS^{14–17}. Additionally, where environmental modifications caused by secondary FS have negative effects on the abundance of one or more species, this may depress the abundance and diversity of the inhabitant community⁵. For example, predatory fish avoid epiphytic seaweeds attached to mangrove roots¹⁴ and seagrass leaves¹⁵, nectar-consuming birds correlate negatively with

dwarf mistletoe abundances on pine trees¹⁶, and seahorses¹⁷ and sediment infauna¹⁸ are inhibited by seaweed mats in seagrass beds and on mussel reefs¹⁹. By contrast, where commensalism or mutualism occurs between secondary and primary FS, community-wide effects of the secondary FS on inhabitants may be positive⁷. For example, the inclusion of epiphytes in surveys in the rainforests of Borneo doubled the estimates of invertebrate biomass relative to a traditional census²⁰. Moreover, recent experimental manipulations of secondary FS in marshes^{8,11}, seagrass beds²¹, mangroves¹⁰ and woodlands²² suggest that secondary FS enhance the diversity and abundance of inhabitants, for example by reducing abiotic stress and predation.

Based on this recent experimental evidence, we hypothesized that co-occurring FS generally increase the richness and abundance of inhabitants compared to the primary FS alone, and that such effects would be apparent regardless of key explanatory variables, including 'structural dependency of the secondary FS on the primary FS', 'plot size', 'latitude', 'ecosystem', 'field methods' or 'type of secondary FS' (see Methods and Supplementary Information Section 1 for details). Knowledge of whether net effects of secondary FS are positive or negative would identify a novel mechanism driving biodiversity patterns, lead to better methods of rapidly assessing changes in biodiversity, and inform the development of more effective conservation and restoration strategies⁶. To assess whether secondary FS modify patterns of biodiversity, we conducted a systematic search for peer-reviewed publications on primary FS-dominated ecosystems that tested, in observational studies or manipulative experiments, whether the presence of secondary FS decreased or increased the abundance or taxonomic richness of inhabitants.

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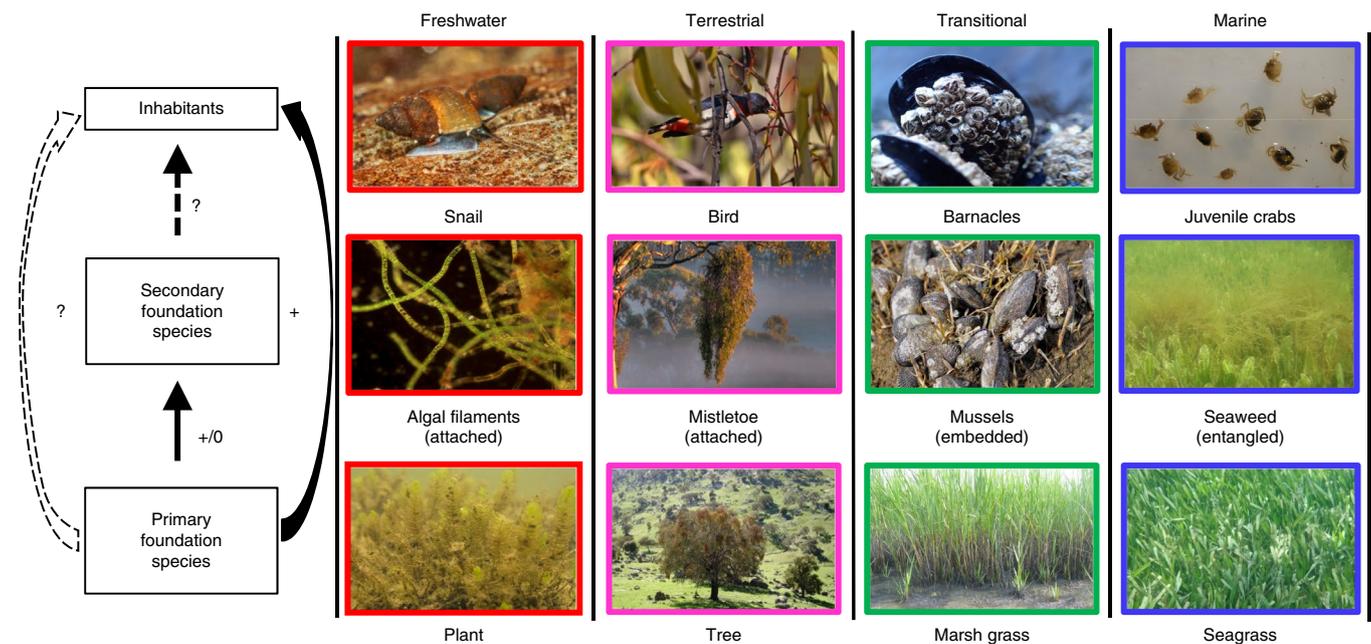


Fig. 1 | Primary and secondary foundation species and their inhabitants: definitions and examples. A FS is 'a species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes'⁴. Several FS often co-occur in nested or adjacent hierarchically structured communities^{7,8,45}. We analysed how nested co-occurrences (that is, where multiple foundation species are found in the same sample) affect inhabitants. Secondary FS were either (1) attached to primary FS (algal filaments attached to freshwater plants by holdfasts; mistletoes penetrating trees with hypocotyls and haustorium^{22,46}), (2) entangled around primary FS (seaweeds trapped by seagrass blades or mangrove pneumatophores; juvenile mistletoes on tree bark) or (3) embedded within primary FS (shell-forming bivalves growing between salt marsh stems or seagrass leaves^{47,48}). These classes reflect the decreasing structural dependencies, contact intimacies and physical forces required to remove the secondary FS. The analysis was framed in a context of co-occurring FS^{41,49}, but co-occurring 'structural species', 'habitat-formers and modifiers'^{7,26}, 'keystone structures'² and 'ecosystem engineers'^{1,5,6} also describe how inhabitants are affected by the sequential formation and modification of biogenic habitat⁷. Most inhabitants and secondary FS can be associated with different FS and non-living structures, but a few have specialized to only inhabit a specific FS^{2,50}. Primary FS have positive effects on inhabitants (solid curved arrow)² and positive or neutral effects on secondary FS (solid straight arrow)^{2,50}, but less is known about how secondary FS (dashed straight arrow) or indirect interactions (dashed bent arrow) affect inhabitants. Many secondary FS (such as mistletoes) and inhabitants (such as birds and limpets) partially consume the FS, but reviewed studies differ from trophic cascade studies, because FS also provide a place to find other resources and facilitators, and to avoid stress and enemies. The reviewed studies described 'sequential biogenic habitat formation' as a contrast to 'sequential consumption'²⁵. These facilitation and habitat cascades are, in contrast to trophic cascades, not described in ecological textbooks, but appear to be pervasive processes modifying biodiversity. Photo credits: snail, plant: A. McIntosh; algal filaments: G. Lear; tree, mistletoe: D. Watson; bird: C. Tzaros; mussels: A. Altieri; other photos: M. Thomsen.

In addition to the explanatory variable tests, we compared our results to published meta-analyses of direct facilitation arising through ecosystem engineering effects from primary habitat-formers¹ (corresponding to the effects of primary FS alone, see Fig. 1) as well as indirect facilitation arising through co-occurring primary and secondary consumer species²³, that is, trophic cascade effects⁷. We compared our results to effects from primary FS because these traditionally studied conspicuous species define many ecosystems, play a critical role in enhancing biodiversity and are typically the targets of conservation and restoration^{1–6}. We hypothesized that effects sizes would be larger for primary FS (compared to no FS) over co-occurring primary and secondary FS (compared to single primary FS), because we expect secondary FS to only add 'a bit more' biogenic biomass and complexity to a system already dominated by biogenic biomass and complexity. In addition, we compared our results to trophic cascade studies because the underpinning ecological processes are relatively similar, involving secondary foundation or secondary consumer species, respectively⁷, and because trophic cascades are considered the sine qua non type of three-tiered indirect species effects, and their conceptual and practical value in ecology is well established^{23–25}. We hypothesized that effects from secondary FS are of similar magnitude to secondary consumers, because habitat formation

and modification, such as consumption, are ecologically important and immediate processes.

Results

We found 91 and 50 papers with relevant abundance and richness data, respectively, from which we calculated 2,187 abundance and 397 richness Hedges' g effect sizes comparing co-occurring primary and secondary FS with primary FS alone. Across all studies, secondary FS significantly increased abundance (mean Hedges' $g = 1.07$, 95% confidence interval (CI) = 0.92–1.23) and richness (mean Hedges' $g = 1.07$, 95% CI = 0.89–1.24).

Despite overall positive mean effect sizes, the heterogeneities for both abundance and richness effect sizes were significant ($P < 0.001$; Supplementary Information Section 2). We explored the causes of these heterogeneities by examining the effects of the following six explanatory variables, individually and in combination: structural dependencies, plot sizes, latitudes, ecosystems, field methods and type of secondary FS.

The effects of secondary FS were generally positive across the six explanatory variables. Specifically, structural dependencies of secondary FS moderated positive effects on inhabitant abundance (Fig. 2a; Cochran's Q -test statistic for the Wald-type test of model coefficients⁴⁴ (Q_M) = 46.3, degrees of freedom (d.f.) = 2, $P < 0.001$)

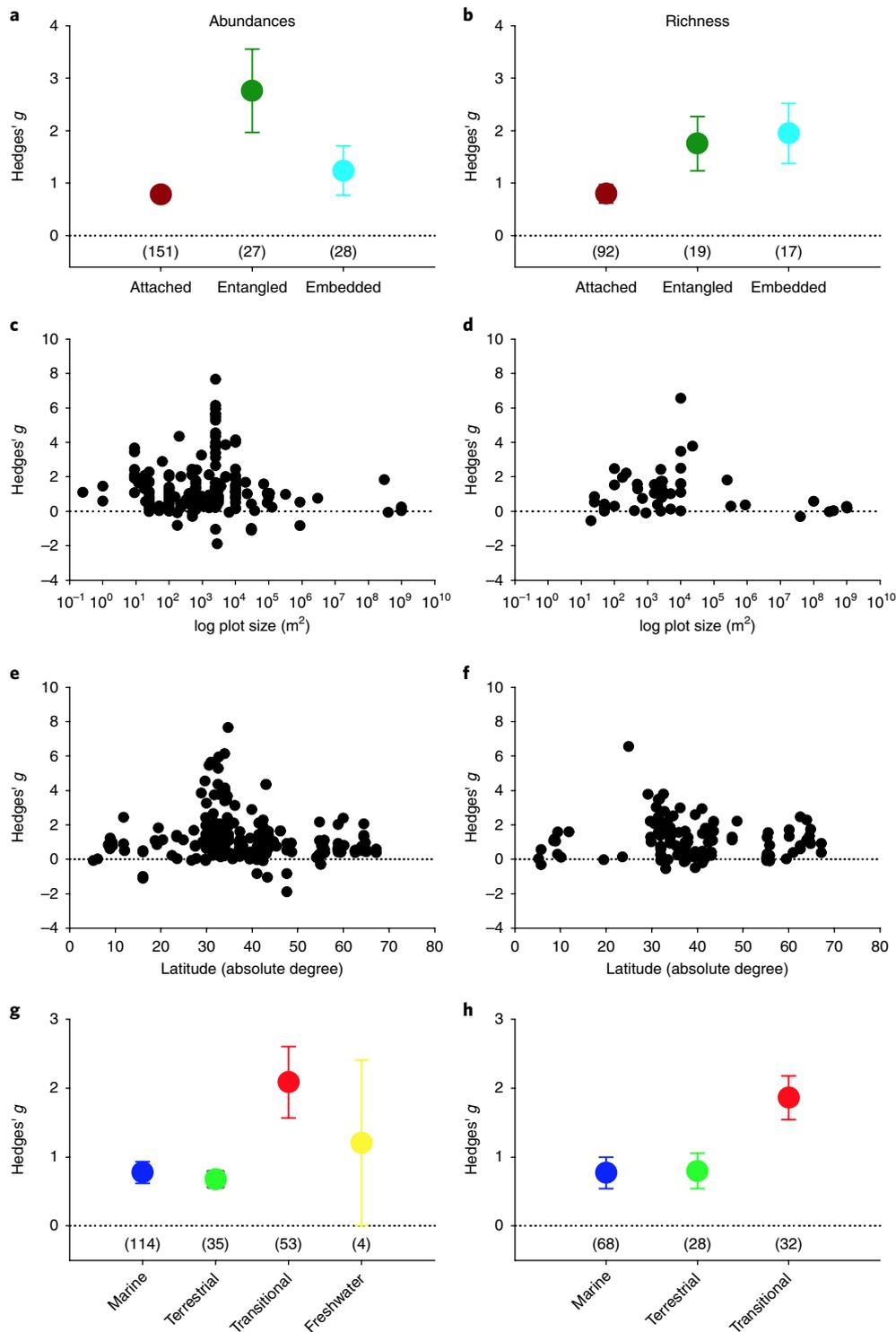


Fig. 2 | Effects of secondary FS on abundance and taxonomic richness of inhabitants. a–h, Effects of secondary FS on abundance (**a,c,e,g**) and taxonomic richness (**b,d,f,h**) of inhabitants, grouped by type of dependency between secondary and primary FS (**a, b**), log plot size (**c,d**), latitude (**e,f**) and ecosystem type (**g,h**). Transitional ecosystems are at the interface of terrestrial and marine systems, such as mangroves and salt marshes. Positive effect sizes occur when co-occurring primary and secondary FS increase the abundance or richness of inhabitants compared to primary FS alone. Error bars are 95% confidence intervals. The numbers of independent effect sizes used to calculate average effect sizes and confidence intervals are shown in parentheses.

and richness (Fig. 2b: $Q_M = 28.8$, d.f. = 2, $P < 0.001$), whereby entangled (Fig. 2a) and entangled and embedded (Fig. 2b) secondary FS exhibited greater effect sizes than attached secondary FS. However, there were no differences in effect size for either abundance or richness among plot sizes (Fig. 2c: $Q_M = 0.74$, d.f. = 1, $P = 0.390$; Fig. 2d:

$Q_M = 0.41$, d.f. = 1, $P = 0.520$) or latitudes (Fig. 2e: $Q_M = 3.69$, d.f. = 1, $P = 0.055$; Fig. 2f: $Q_M = 0.36$, d.f. = 1, $P = 0.549$), although effect sizes tended to be small at particularly large plot sizes (Fig. 2c,d). This may reflect a saturation of species–area relationships with increasing spatial scale, or methodological challenges associated with maintaining

experimental treatments and with quantifying biodiversity at large scales. We also found that ecosystem type moderated the effects of secondary FS on inhabitant abundance (Fig. 2g: $Q_M=36.1$, d.f. = 3, $P<0.001$) and richness (Fig. 2h: $Q_M=36.3$, d.f. = 2, $P<0.001$), with secondary FS having stronger effects in transitional ecosystems characterized by strong intertidal stress gradients in temperature and desiccation^{10,11} than fully marine and terrestrial ecosystems. Additionally, effect sizes were similar between observational and experimental studies for both inhabitant abundance ($Q_M=1.65$, d.f. = 1, $P=0.199$) and richness ($Q_M=0.29$, d.f. = 1, $P=0.588$), demonstrating that secondary FS facilitation effects are consistently detected, regardless of field methods. Finally, effect sizes were also similar between live secondary FS and structural analogues for both inhabitant abundance ($Q_M=1.57$, d.f. = 1, $P=0.210$, Supplementary Information Section 2) and richness ($Q_M=3.32$, d.f. = 1, $P=0.068$, Supplementary Information Section 2). This result suggests that the effects of secondary FS arise primarily through their provision of habitat structure, which may increase habitat space and modify environmental conditions.

We also used an information-theoretic approach to evaluate the potentially non-independent and interactive effects of five of the six explanatory variables (except 'type of secondary FS', due to the small sample size) in factorial meta-regression models (see Methods). This analysis confirmed that the relative strength of the effects of secondary FS was better predicted by a combination of multiple factors. The effect size of secondary FS on inhabitant abundance, for example, was best predicted by the combination of structural dependency, plot size, ecosystem, field method and interactions of structural dependency with plot size, ecosystem and field method. This combination of explanatory variables similarly affected the effect size of secondary FS on inhabitant richness, although this effect size was also affected by latitude, its interaction with the field method, and an interaction between ecosystem and plot size (see Supplementary Information Sections 1 and 2 for details).

Despite some variation in the magnitude of positive effects, we found that secondary FS enhance the abundance and richness of inhabitants across structural dependencies, plot sizes, latitudes, ecosystems, field methods and types of secondary FS, in habitats ranging from rainforests to seagrass beds, and at spatial scales spanning ten orders of magnitude from individual seagrass blades⁹ to entire wetlands²⁶. Indeed, in not one instance did we find an average negative effect size of secondary FS for any test factor.

So far, an extensive literature has documented direct facilitation arising from primary FS^{1,2,26} as well as indirect facilitation mediated by primary and secondary consumers in the sequential negative species interactions of trophic cascades^{23,25}. Our analyses show that the strength of indirect facilitation of inhabitants arising through sequential habitat formation and secondary FS (this study) is similar in magnitude to direct facilitation arising from primary FS (see the richness data from the online supplement in ref. 1: $Q_M=0.18$, d.f. = 1, $P=0.672$, secondary FS = 0.57, 95% CI = 0.41–0.73, $n=91$ vs primary FS = 0.51, 95% CI = 0.31–0.72, $n=144$) and significantly greater than indirect facilitation of plants arising through trophic cascades (see abundance data from the online supplement in ref. 23: $Q_M=22.3$, d.f. = 1, $P<0.001$, secondary FS = 1.15, 95% CI = 1.03–1.27, $n=231$ vs secondary consumer species = 0.61, 95% CI = 0.42–0.80, $n=112$). However, these tests were carried out as unweighted analyses and should therefore be interpreted with caution²⁷. Nevertheless, these findings suggest that, on average, the effect of sequential habitat formation by secondary FS on species richness can be comparable to primary FS¹, and their effect on species abundances possibly greater than that of trophic cascades²³.

Discussion

The enhancement of diversity by secondary FS suggests that, relative to primary FS on their own, they augment the quantity and/

or quality of habitat available for inhabitants to avoid enemies and stress and/or to find resources and facilitators^{3,7,28}. Unfortunately, we could not explore the detailed mechanisms underlying secondary FS effects on inhabitants because most studies did not present the required variables for assessment. These variables would include surface areas, weights, volume, fractal dimensions, hardness or palatability of both the primary and secondary FS, or the extent to which they independently and collectively ameliorate environmental and/or biotic stressors.

If habitat space is a limiting resource, secondary FS should have density-dependent positive effects on the abundances of inhabitants^{8,11,22} and might also increase species richness through sampling effects²⁹. In this case, the effect of secondary FS should be apparent regardless of whether live secondary FS or structural analogues are manipulated. However, if inhabitants also consume secondary FS (in addition to depending on their physical attributes, for example through stress reduction), then more inhabitants should be associated with live secondary FS than structural analogues. The absence of a significant difference in the effect size of live secondary FS and structural analogues suggests that the effects of secondary FS arise primarily through their provision of habitat structure, which may increase habitat space and modify environmental conditions. Furthermore, although the hypothesis of habitat limitation was not addressed in this meta-analysis, several studies have shown stronger facilitation when secondary FS are added in greater densities^{10,11,21}.

Although our results highlight strong positive effects of secondary FS on inhabitant richness at scales from leaves to entire forests, it is unknown whether secondary FS affect regional species richness (gamma diversity). Most studies showed that inhabitants associated with secondary FS are also found, albeit less frequently, on primary FS^{7,8,10,11,22}, indicating that inhabitants typically have low host specificity. However, where the secondary FS differs from the primary FS in key morphological or functional traits, it may enhance species richness by adding new niches through habitat heterogeneity^{7,8,11,13}, or novel resources such as enriched litter fall year round from parasitic mistletoes³⁰ or persistent micro-ponds in water-holding epiphytic tank bromeliads^{31,32}. Nevertheless, instances where secondary FS primarily increase inhabitant abundances rather than richness³³ are still of ecological relevance because larger population sizes generally enhance genetic diversity³⁴ and resilience to disturbances and extinctions³⁵, and can function as a trophic resource or demographic source for adjacent systems³⁶. Recent studies have also indicated that by amplifying local biodiversity, secondary FS play an overlooked role in enhancing the complexity of interaction webs as well as elevating ecosystem functions and multifunctionality at local and landscape scales^{11,37}.

Our analysis also highlights research gaps regarding the ecological effects of secondary FS. To address these research gaps, we suggest five key areas for future research. First, we suggest that new studies identify thresholds in secondary FS density above which primary FS are negatively affected and the net effect on inhabitants switches from positive to negative. Such breakdowns of positive interactions occur in marine systems where nutrient-fuelled overstimulation of epiphytes converts seagrass beds to species-poor mudflats³⁸. Second, we recommend that studies report the abundances of co-occurring FS with commensurable metrics, and aim to identify mechanisms by which secondary FS affect inhabitants. It is, for example, important to know whether inhabitants use secondary FS as a point of attachment, to find food and facilitators, or to avoid stress and enemies. Third, we advocate that studies determine the host specificity of the secondary FS and inhabitants¹² and test whether host specificity affects the stability of biodiversity enhancement. Fourth, we suggest that, to decrease study bias, future investigations target the test categories that have had the fewest studies, such as embedded secondary FS, freshwater ecosystems, equatorial and polar latitudes, and very large plot sizes. Finally, we recommend

that more studies quantify the effects of secondary FS and inhabitants on ecosystem processes, such as nutrient cycling and energy transfer, and on the structure and stability of interaction webs^{11,21,36,37}.

Our finding that the presence of secondary FS enhances the abundance and richness of inhabitants has important implications for biodiversity assessment, conservation and management. For example, consideration of the effects of secondary FS in assessments of biodiversity will lead to more effective decisions about where best to commit resources to preserve and enhance biodiversity⁶. In ecosystems where secondary FS are not uniformly distributed within primary FS, managers could prioritize areas of high levels of secondary FS because these are likely to be biodiversity hotspots¹⁵ with spillover effects on adjacent communities³⁶. Furthermore, our findings indicate that current assessments of global biodiversity distribution and rates of biodiversity loss may change substantially because many local estimates ignore the effects of secondary FS³⁰, or the potentially nonlinear consequences that their loss could have on biodiversity^{10,11}. Similarly, we anticipate that restoration projects based on the rehabilitation of both primary and secondary FS will foster synergistic biodiversity benefits. Secondary FS are already being incorporated into large-scale restoration and ecological engineering projects as an effective shortcut to help rebuild ecosystems, even under conditions where the primary FS are no longer supported³⁹.

Given their prevalent role across scales, latitudes and ecosystems, we recommend that secondary FS are included as part of a unified framework in both theoretical ecology and biological conservation, alongside other indirect interactions⁷ such as trophic cascades. This will provide a greater depth of understanding of key diversity drivers and a more holistic basis on which to maintain and manage biodiversity.

Methods

The meta-analysis followed PRISMA guidelines (Supplementary Information Section 1 and Supplementary Fig. 2). Using complementary literature searches (Supplementary Information Section 1) we identified 91 and 50 peer-reviewed publications that tested whether co-occurring primary and secondary FS affect the abundance and richness of inhabitants, respectively, as compared to primary FS alone. Studies were carried out in 32 countries on all continents except Antarctica (with the majority coming from the USA and Australia). The reviewed publications were primarily about attached and entangled secondary FS, but also included case studies with embedded secondary FS that are more difficult to identify with standardized search criteria (see Supplementary Information Section 1 for details).

We extracted data on the abundance and taxonomic richness of inhabitants of primary FS alone and co-occurring primary and secondary FS, to calculate 2,187 and 397 Hedges' *g* effect sizes^{27,40} for abundances and taxonomic richness, respectively. Hedges' *g* was calculated as the abundance or richness of ((co-occurring primary and secondary FS – primary FS alone)/*S*) × *J*, where *S* is the pooled standard deviation and *J* is a factor that corrects for bias associated with small sample sizes (see ref. ⁴⁰ for full formulae).

Negative or positive effect sizes occur when co-occurring primary and secondary FS decrease or increase the abundance or richness of inhabitants, compared to primary FS alone, respectively. Prior to meta-analyses, non-independent within-study effect sizes were averaged (1) across repeated measurements, (2) for multiple densities of the primary or secondary FS, (3) for multiple FS and inhabitants, (4) for multiple responses per inhabitant, and (5) across nested and orthogonal experimental designs, for example across seasons and water depth levels (see Supplementary Information Section 1 for details).

We used weighted random-effects models^{27,40} to test whether effect size varied with each of the six explanatory variables, including the type of secondary FS dependency (that is, whether the secondary FS was attached to, entangled around, or embedded within the primary FS), spatial scale (plot size), latitude and ecosystem (see Supplementary Information Section 1 for details). Ecosystems were categorized as terrestrial, marine, freshwater or transitional, where the latter are boundaries between terrestrial and marine systems, such as mangroves and salt marshes. In addition, we also tested if effect sizes varied with field method (observational studies vs manipulative experiments) and type of secondary FS (living vs non-living structural analogue of secondary FS)⁴¹. Most studies did not quantify biomass, volume, surface area or other comparable traits of the primary and secondary FS^{8,22} and it was therefore not possible to test in detail whether negative (or positive) effects on inhabitants depended on quantitative (for example, amount or size) or qualitative (for example, shape, chemicals or biomechanical properties) differences between the co-occurring primary and secondary FS.

Because it is likely that explanatory variables were non-independent of each other and that interactions occurred between the explanatory variables, we further evaluated the performance of a candidate set of factorial meta-regression models. This set of models related effect sizes to the main and two-way interactive effects of five of the six explanatory variables (not the type of secondary FS structural analogue, due to the small sample sizes) in all possible combinations. The type of secondary FS, which compares living organisms to structural analogues, was not included in the model selection procedure, because only 10 and 3 studies, respectively, reported the abundances and richness of inhabitants on non-living structural analogues of secondary FS. We precluded any potential effect of this explanatory variable by considering only studies of living secondary FS. The most parsimonious models in predicting variations in effect size were selected using Akaike's information criterion, corrected for small sample sizes (AICc)⁴².

We examined the potential influence of publication bias in multiple ways. First, we examined funnel plot asymmetry for each effect size metric using the trimfill method and regression tests (see ref. ⁴² for methodological details). We also calculated the fail-safe number using the Rosenberg method, which estimates the number of studies averaging null results that would have to be added to the given set of observed outcomes to reduce the significance level (*P* value) of the (weighted) average effect size (based on a fixed-effects model) to a target alpha level (that is, *P* = 0.05)^{40,43}. The results from these tests suggest that publication bias has limited effects and that our results are robust (Supplementary Information Sections 1 and 2).

In addition, we carried out a full set of matching unweighted analyses based on the log response ratio (ln(co-occurring primary and secondary FS/primary FS alone))⁴⁰, including studies that reported effects without associated data dispersion (using a unit variance of 1 and bootstrapped confidence intervals). These analyses were important because more primary studies could be included (104 papers for abundance and 57 for richness), increasing the taxonomic and spatio-temporal generality of our conclusions. However, unweighted analyses are less statistically robust than weighted analyses and should be interpreted more cautiously²⁷. Nevertheless, the ecological conclusions derived from the unweighted analyses fully support the conclusions based on the weighted analyses: all mean effect sizes were positive, demonstrating that secondary FS facilitate inhabitants across moderator tests and analytical methods (Supplementary Information Section 2).

Finally, we statistically compared our log response ratios to log response ratios reported in online supplements of published meta-analyses of ecosystem engineering effects on species richness⁴ and trophic cascade effects on abundances²³ (we only used the effect sizes reported for 'habitat-forming engineers' in ref. ⁴ because habitat-forming engineers are ecologically very similar to FS; Fig. 1). Many log response ratio values were reported without data dispersion, so the two complementary analyses were carried out as unweighted analyses and significant effects should be interpreted cautiously²⁷.

Weighted Hedges' *g* analyses and the publication bias tests were carried out in R 3.4.2, using its metafor⁴⁴ and glmulti⁴⁵ packages, whereas unweighted log response ratio analysis and calculations of bootstrapped confidence intervals were performed in MetaWin 2.1⁴⁶.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. All data generated or analysed during this study are included within the paper and its Supplementary Information and Supplementary Data files.

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Author contributions

M.S.T. identified relevant literature, extracted all data and calculated effect sizes. M.S.T. and Q.H. analysed the data. All authors contributed to the development of the experimental design, data interpretation and manuscript.

Competing interests

The authors declare no competing financial interests.

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

Sample size was determined from standardized data extraction of published experiments identified from 2 standardized literature searches (based on standardized search terms) combined with an expert-based search.

2. Data exclusions

Describe any data exclusions.

No data points were excluded that fulfilled our standardized data selection criteria/searches (see S1 for details).

3. Replication

Describe whether the experimental findings were reliably reproduced.

Results from weighted random effect models (based on Hedges' g effect sizes) presented in the manuscript were supported by results from unweighted analysis of Ln RR effect sizes presented in the online supplement. Results were also supported when analyses were run based on less conservative pooling procedure of non-independent effect sizes (e.g., if multiple effect sizes were used from orthogonal or nested experimental designs instead of using their average effect size).

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

NA (meta analysis)

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

50 randomly selected effect sizes were extracted from the peer reviewed publications on two occasions, revealing low extraction variability (Supplement 1)

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

- | | |
|-------------------------------------|--|
| n/a | Confirmed |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The <u>exact sample size</u> (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.) |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A statement indicating how many times each experiment was replicated |
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| <input type="checkbox"/> | <input checked="" type="checkbox"/> A description of any assumptions or corrections, such as an adjustment for multiple comparisons |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range) |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> Clearly defined error bars |

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

Statistical software R with metafor and glmulti packages (and Metawin 2.1 for un-weighted analyses shown in Supplement)

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). [Nature Methods guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

We present data used for all analyses in the supplementary material.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No cell lines were used.

b. Describe the method of cell line authentication used.

No cell lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

No cell lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No cell lines were used.

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

No animals were used.

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

No human participants were involved.