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Reciprocal knowledge exchange between climate-driven species redistribution and invasion ecology

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Abstract

Climate change is driving a rapid but highly variable redistribution of life on Earth, comparable in scale and magnitude to changes historically only seen over tens of thousands of years. Despite increased research effort, the complex mechanisms driving these changes in geographical distribution of species, or 'range shifts', remain only superficially understood. Attempts to understand the processes underpinning species responses are hampered by the paucity of comprehensive, longterm datasets, few theoretical frameworks, and lack of strategic direction and cross-fertilisation with related ecological fields. As an emerging, dynamic field, range shift ecology would benefit from integrating concepts and approaches from other related, more established areas of research, such as invasion ecology. Here, we use a systematic literature review and bibliographic analysis to assess the level of knowledge exchange between range shift ecology and invasion ecology. We found that while the two fields are inherently strongly related, the level of exchange and integration of ideas via citation networks does not reflect the closeness of the fields in terms of concepts, theories, and practice. Although range shift papers cite invasion papers more often than vice versa, the citation rate is generally quite low for both. These findings are evidence of the increasing need to move away from discipline-focused interpretation and communication of scientific results, towards greater research integration and connection between related ecological fields. Increased knowledge and data exchange between range shift and invasion fields could improve mechanistic understanding of range shifts and species invasions under climate change, enhance the predictive capacity of models and better inform management and conservation efforts.

Highlights

- Range shifting species and invasive species share many key processes and theories
- Bibliographic analysis (using keyword co-occurrence, bibliographic coupling, and direct citations) can detect the degree of cross-fertilisation between fields
- Current knowledge exchange between range shift ecology and invasion ecology is limited, even within related sub-fields such as climate-driven species movement
- Increased reciprocal exchange between related ecological fields could can advance understanding and improve management outcomes in the face of accelerating global change

Keywords: bibliographic analysis, climate change, climate-driven range shift, global change ecology, invasive species, species redistribution

Introduction

Climate change is causing a rapid redistribution of life on Earth (Pecl et al. 2017). Increasing temperatures on land and in the upper ocean are triggering species to shift their geographical distribution (range) in order to remain within their thermal niche. As global surface temperatures are expected to continue to increase until at least the mid-century, species shifts are projected to accelerate (Bonebrake et al. 2018, IPCC 2021). In addition to other anthropogenic drivers of biodiversity change (e.g., invasive species, habitat loss, overexploitation, pollution; Díaz et al. 2019), climate-driven species redistributions (herein referred to as range shifts) are leading to a reshuffling of biodiversity (Moor et al. 2015, Pecl et al. 2017, Vincent et al. 2019, Alabia et al. 2020). Many species are shifting their distribution across elevational and latitudinal gradients, tending to move to higher latitudes (poleward), greater elevations (for terrestrial species) and greater depths (for aquatic taxa; Parmesan and Yohe 2003, Sorte et al. 2010, Pinsky et al. 2013, Lenoir and Svenning 2015, Poloczanska et al. 2016, Scheffers et al. 2016, Pecl et al. 2017). However, the nature of biodiversity change is highly contextdependent; while some biomes show species loss, others show increasing diversity. For example, tropical marine biomes are emerging as hotspots of lost species richness, whereas temperate marine locations tend to show richness gains (Blowes et al. 2019, Antão et al. 2020). In order to anticipate the direction and magnitude of biodiversity change, it is therefore essential to understand in detail the processes of this large-scale reorganisation of global biodiversity, as well as the resulting impacts on organisms, ecosystems and human societies (Blowes et al. 2019, Eriksson and Hillebrand 2019).

Range shift ecology has emerged within the last two decades in an attempt to understand, explain and predict climate-driven range shifts, and their impacts on donor and recipient communities (Southward et al. 1995, Pecl et al. 2017). Despite increased research effort in recent years, the complex processes driving range shifts remain poorly understood (Bonebrake et al. 2018). How each species responds to climate change is highly contextspecific, governed by a unique mix of individual traits, abiotic and biotic factors, genetic processes, habitat connectivity and phenotypic plasticity (Whitmee and Orme 2012, Estrada et al. 2016, Williams and Blois 2018, Platts et al. 2019, Beissinger and Riddell 2021, García Molinos et al. 2022). Attempts to understand the processes underpinning species responses are further hampered by the paucity of comprehensive, long-term datasets for different biological systems (Poloczanska et al. 2013). It is becoming increasingly clear that range shift ecology requires strategic direction and interdisciplinary collaboration, as integrated frameworks for predicting range shifts remain scarce in the literature (Bonebrake et al. 2018, Twiname et al. 2020, Hof 2021, Henry and Sorte 2022). As an emerging, dynamic field, range shift ecology could benefit from integrating concepts

and approaches from other related, more established research fields (Gilman et al. 2010, Twiname et al. 2020).

Range shifts and expansions of invasive species share many similarities, as both phenomena are widespread globally, involve movement of individuals from a donor to recipient community, and are susceptible to the influence of climate change (Sorte et al. 2010). As such, invasion ecology – the study of human-mediated introduction of organisms to areas outside of their native range (Richardson and Pyšek 2007) – shares many key processes and theories with range shifts (Theoharides and Dukes 2007, Sorte et al. 2010, Bates et al. 2014). Some successful range-expanding species also exhibit traits commonly associated with invasive species (Engelkes et al. 2008, Tracey et al. 2015), such as broad physiological tolerances, phenotypic plasticity, ecological generalism and ability to overcome barriers to dispersal (Angert et al. 2011, Weir and Salice 2011, Bates et al. 2013, Bates et al. 2014). Furthermore, the impacts of species range shifts on ecological communities can be similar in mechanism and magnitude to those of invasive species introductions (Sorte et al. 2010, Wallingford et al. 2020), having the potential to be beneficial (e.g., maintaining or even enhancing ecosystem processes in the absence of native species; Mascaro et al. 2012, Pessarrodona et al. 2019), or detrimental (e.g., out-competing native species; Tracey et al. 2015, Vergés et al. 2016). These similarities make invasion ecology a prime candidate for reciprocal knowledge exchange with range shift ecology.

While examples of reciprocal knowledge exchange between fields of research are becoming more common in scientific literature (Soininen et al. 2015, Wallingford et al. 2020, Latombe et al. 2021), many related fields in ecology still suffer from a lack of "cross-fertilisation", particularly between different ecosystems (Menge et al. 2009, Orr et al. 2020, Hof 2021). This problematic trend is highly apparent between marine and terrestrial ecology (Menge et al. 2009, Webb 2012, Rotjan and Idjadi 2013, Wirsing et al. 2014, Soininen et al. 2015), as aquatic publications cite terrestrial research approximately 10 times more often than vice versa (Menge et al. 2009, Soininen et al. 2015). Similarly, low levels of integration within global change biology have created a divide between the fields of physiology, dispersal and land-use change (Hof 2021). In the context of climate change, a disconnect between related areas of research can hamper understanding of the biodiversity responses to global change and impede efforts to mitigate negative effects and conserve ecosystem functioning (Ruttenberg and Granek 2011, Knapp et al. 2017). Thus, ensuring that range shift ecology is well-integrated with other closely related fields is an important step to advancing our understanding of range shifts and their impacts to biodiversity and the delivery of ecosystem services.

While it is clear that there is great potential for reciprocal exchange between range shift and invasion ecology, there have not yet been attempts to quantify and examine the level of knowledge exchange between the two fields. Thus, it is not known to what extent exchange is currently occurring, or what capacity there is for future exchange. The aim of this study was to examine the current degree of cross-fertilisation between range shift ecology and invasion ecology, as a first step in determining the level of need for increasing connection between the two fields. Research of this nature will not only highlight the commonality and division between the two fields, but also serve to solidify the connection between the two research communities, setting the scene for further reciprocal learning opportunities and information exchange within climate change ecology.

To that end, here we examine (1) the structure and degree of similarity of themes explored within range shift and invasion ecology publications, (2) the extent that range shift and invasion publications draw on a common pool of research, and (3) the extent that range shift and invasion publications directly cite publications from the other field of study.

Materials & Methods

To assess the level of knowledge exchange between range shift and invasion ecology and evaluate the hypothesis that there is an overall low level of integration between the two fields, we undertook a systematic literature review. Bibliographic analyses were based on the methods employed by Hof (2021) and Orr et al. (2020), which more generally assessed integration with biological climate impact research communities and multiple stressor research, respectively.

Systematic literature review

An automated approach was applied to identify search terms for a systematic literature review. Ecological fields generally lack standardised terminology; therefore it was crucial to utilise a search strategy that accounted for synonymous phrases in search terms (Grames et al. 2019).

Search term identification

A naive list of search terms relating to range shifts and invasion ecology was used to conduct an initial search of Scopus (https://www.scopus.com) and Clarivate Web of Science (https://webofknowledge. com) databases, for publications using any of the key search terms in the title, abstract or author keywords. The publications returned by this search were then analysed in R (https://www.r-project.org/) using the *litsearchr* package (Grames et al. 2019). This package uses text-mining and keyword occurrence networks to generate comprehensive lists of key search terms, thereby reducing bias and helping to identify terms that might otherwise be missed. Search terms were refined further and separated based on discipline (Table 1).

Literature search

Each list of terms was used to perform a search of range shift and invasion ecology literature in the Scopus database. Searches were performed on 8-10 June 2021. Each search was limited to primary literature published between 1996 and 2020, using any of the key search terms in the title, abstract or author keywords. The year 1996 was chosen as the first year of the search period as it represents the point at which more than one document per year relating to climate-driven range shifts was published. Publications were further limited to Agricultural and Biological Sciences, Environmental Science, Biochemistry, Earth and Planetary Sciences, and Multidisciplinary subject areas. Publications in languages other than English, as well as those without abstracts, were excluded. To reduce the final number of publications analysed, minimum citation cut-offs were applied to remove papers with low citations. For years 1996–2018, publications with fewer than 10 citations were excluded. For years 2019 and 2020, publications were excluded if they had been cited fewer than five and three times respectively. After minimum citation cut-offs were applied, publications were grouped into five-year periods (1996-2000, 2001-2005, 2006-2010, 2011-2015, 2016-2020) (Table 2).

Owing to the large number of publications returned from the search of Scopus, it was not possible to analyse all publications. Therefore, the number of papers examined varied based on the method of analysis conducted (Table 2). Further details outlining choices behind variable sample sizes used be certain analyses are provided in subsequent sections.

Bibliographic analysis

Keyword co-occurrence

The use of keywords across range shift and invasion papers were evaluated to determine the degree of shared themes between the two fields. Publication

Table 1. Search criteria used to perform a qualitative literature review of range shift and invasion ecology literature. Searches were performed using specific terms and Boolean operators.

Торіс	Search terms					
Range shift	Title or Abstract or Keyword = (specie* redistribut* OR climate-driven* speci* redistribut*) OR ((climat* chang* OR climate*driven OR global warm*) W/3 (rang* expans* OR rang* contract* OR speci* shift* OR rang* shift* OR speci*					
	distribut* OR dispers*))					
Invasion ecology	Title or Abstract or Keyword = (biolog* invas* OR introduc* speci* OR invas* speci* OR speci* invas* OR invas* impact* OR non-indigen* speci*)					

Total

1102

Year	(A) Returned by search		pling, and (E) analyse (B) After minimum citation cut-off		(C) Keyword co-occurrence		(D) Bibliographic coupling		(E) Citation network	
	RS	INV	RS	INV	RS	INV	RS	INV	RS	INV
1996-2000	19	1400	12	1165	12	12	0	0	0	0
2001-2005	33	3944	13	3304	13	13	0	0	0	0
2006-2010	155	9798	89	6862	89	89	0	0	0	0
2011-2015	345	15265	243	9454	242	242	0	0	0	0
2016-2020	550	18467	268	6369	268	268	268	1592	268	1592

624

624

268

Table 2. Sampling effort for each analysis. Number of range shift (RS) and invasion (INV) publications per five-year period, (A) returned by search of Scopus, (B) remaining after citation cut-off applied, (C) analysed using keyword co-occurrence, (D) analysed using bibliographic coupling, and (E) analysed using citation networks.

titles and abstracts were read to ensure only relevant papers were analysed. To be considered relevant, the main focus of the publication had to be related to range shift or invasion ecology (i.e. not relating to invasive medicine/immunology/pharmacology etc.). Publications that made only passing mention of range shift or invasion ecology in the abstract were excluded. While it was possible to read the abstract of all range shift publications (n = 845), due to time and resource limitations, it was impractical to read all invasion publications (n = 27154). A random sample of invasion publications was selected for each period, with the total number of publications selected for each period matching the number of range shift publications for that same period (Table 2). Publications were combined into a single dataset for analysis (n = 1248). For simplicity, keywords with multiple forms were replaced with a shortened form (Table S1).

48874

625

27154

Papers containing common terms imply a common research topic (Morris and Yen 2004); thus, keyword co-occurrence analysis was used to describe the knowledge structure and visualise relationships between the two fields (Yang et al. 2016). Relationships between author keywords were analysed using cluster and ordination techniques performed by the bibliometrix package (Aria and Cuccurullo 2017) in *R*. Using the *conceptualStructure* function, multiple correspondence analysis (MCA) and clustering was performed to draw a conceptual structure and clustering dendrogram of the 90 most common author keywords (numbers restricted for clarity). The relatedness of keywords was determined based on the number of documents in which they occur together.

Clustering algorithms performed within VOSviewer (van Eck and Waltman 2010) (version 1.6.17.0) were used to construct a co-occurrence network of the same 90 author keywords. Nodes were coloured according to research topic and weighted based on occurrences.

Bibliographic coupling

To evaluate the extent that publications share sources and thus have similar research interests, bibliographic coupling analysis was conducted within

VOSviewer using range shift and invasion literature published between 2016 and 2020 (Table 2). All final range shift publications from this period were used (n = 268). The number of invasion publications from this period was too large for sensible visualisation (n = 6,369), therefore a subset of publications, where a secondary, higher citation cut off (minimum citations = 22, n = 1592) was applied to invasion publications, was used for network visualisation. Invasion publications with lower citations were excluded as they have a lower capacity for bibliographic coupling. The remaining invasion publications were combined with range shift publications into a single dataset and analysed using citation analysis (Table 2). From this dataset, bibliometric analysis selected the largest bibliographically-coupled network of 1800 publications for viewing. Two publications were considered to be bibliographically coupled if at least one cited source appeared in the reference lists of both articles (Kessler 1963). Publications were manually assessed to determine which research field they belonged to, and nodes were coloured accordingly for visualisation.

1592

268

1592

Citation networks

In order to determine the amount of direct exchange between publications, citation analysis was conducted within *VOSviewer* using publications from 2016–2020. A number of citation networks were constructed to investigate the relationship between direct citation links and number of citations publications have accrued.

First, general patterns were explored by utilising all range shift publications and a random subset of invasion publications. Three random subsets were tested to check for consistency in the results. To create these networks, 1592 invasion publications (number limited by *VOSviewer*) were randomly chosen from all papers published between 2016 and 2020 (Table 2) and combined with all 268 range shift papers from that period. From these datasets, clustering algorithms and citation analysis were used to create citation networks. As the networks tended to consist of lots of small clusters (approximately 20-30 publications), 904 of the highest connected papers were selected to create each network, in order to depict the level of exchange more accurately.

To investigate citation patterns among more highlycited papers, three more citation networks were constructed using: i) all 268 range shift publications and 1592 invasion ecology publications with at least 22 citations; ii) all 268 range shift ecology publications, and 888 invasion ecology publications with at least 30 citations; and iii) 50 range shift ecology publications with at least 30 citations, and 888 invasion ecology publications with at least 30 citations. From these datasets, the largest connected networks were analysed.

To analyse the networks, the research field of each publication was manually assessed, and nodes coloured accordingly. Citation links occurred between two publications when one publication cited the other. When a citation link occurred, the direction of the citation (i.e., range shift citing invasion or vice versa) was determined using publication age. When two linked publications were published within the same year, publication reference lists were examined to determine the citation direction. As citations were counted using publication reference lists, citation links were binary (ie., links did not indicate whether a publication cited another publication once or multiple times within the text).

Results

Keyword co-occurrence

Cluster analysis and ordination revealed that there were distinct and separate keyword clusters between

range shift and invasion literature (Fig. 1). The largest of the clusters (n = 42) contained author keywords relating to a broad range of topics. This cluster consisted of keywords relating to climate-change, range shifts, species redistribution modelling, and some more general terms (e.g. citizen science, functional traits, biogeography).

The range shift cluster was most closely related to the second-largest cluster (Fig. 1; n = 36), which mostly consisted of author keywords relating to invasion ecology. All invasion-specific keywords were contained within this cluster. Most general terms related to monitoring and management of invasive species (e.g., biological control, biosecurity, risk assessment).

The invasion and range shift clusters were best separated along the first axes, which accounted for 22% of variability in the data. The smaller third (n = 5) and fourth (n = 7) clusters, containing population and landscape-scale terms, respectively, were separated along a second axis that contained only 9.5% of variability in the data (Fig. 1).

Further examination using co-occurrence networks revealed some integration of range shift and invasion keywords (Fig. 2). Invasion keywords (n = 15) formed a cluster within the keyword network. In contrast, range shift keywords (n = 4) were widely dispersed throughout the network. Range expansion was positioned close to the invasion cluster, while all other range shift keywords were located far from invasion keywords. Most general keywords (Fig. 2) were linked to keywords from both research topics. Climate change was central relative to both fields, but more fully embedded within range shift keywords.

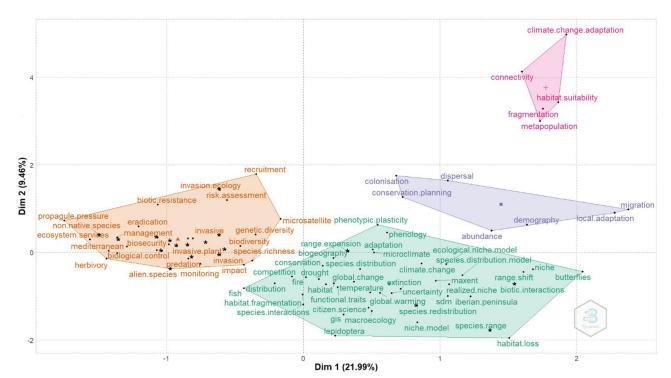


Figure 1. Conceptual structure of the 90 most frequently co-occurring author keywords used within range shift ecology and invasion ecology literature published between 1996 and 2020, given by multiple correspondence analysis. Points marked by an asterisk (*) depict author keywords identified as specific to range shifts or invasions.

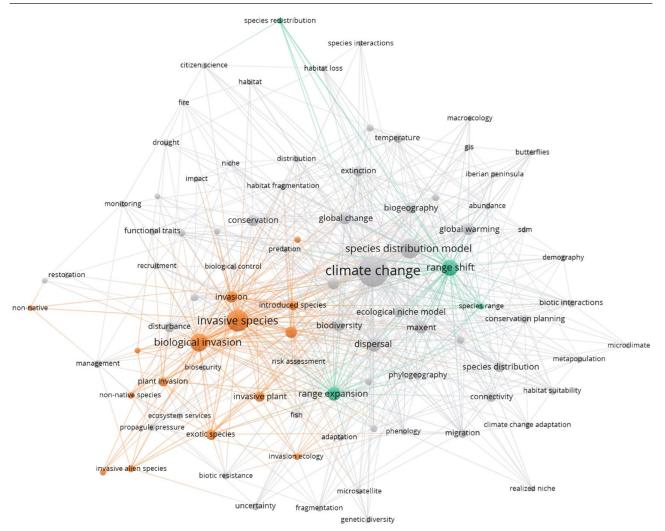


Figure 2. Keyword co-occurrence network of the 90 most frequently co-occurring author keywords used within range shift ecology and invasion ecology literature from 1996 to 2020. Nodes are coloured based on research topic (teal = range shift, orange = invasion ecology, grey = general terms). Node size represents keyword occurrences, defined as the number of publications in which a keyword occurs. Links indicate co-occurrence of keywords within a publication. The relatedness of keywords is determined by the number of times they co-occur, represented as the distance between nodes.

The most frequently occurring keywords (indicated by node size) were climate change (289 occurrences), invasive species (122), species distribution model (102), biological invasion (83) and range shift (64). These keywords also exhibited the highest number of keyword links (72, 48, 61, 46 and 43 links, respectively).

The number of keyword links were calculated for the two most frequently occurring keywords from the field of range shift ecology ("range shift" and "range expansion") and invasion ecology ("invasive species" and "biological invasion") (Fig. 3). All four keywords were most commonly linked with general keywords. Range expansion showed the highest number of links to invasion keywords, whereas range shift, invasive species and biological invasion keywords had low numbers of links with keywords from the other research fields.

Bibliographic coupling

The largest connected bibliographic coupling network consisted of 260 range shift publications and 1540 invasion publications. Owing to the high rate of coupling, it was not possible to count the number of coupling links between range shift and invasion publications; however, general trends were apparent.

The majority of invasion publications (Fig. 4) were contained within one main cluster. Two minor clusters formed on the periphery of the network, connected to the main cluster via a small number of key nodes. Range shift publications formed a cluster that was integrated within an area of the main invasion cluster. Despite there being far fewer range shift publications within the network, most range shift nodes (node size representing number of links to other publications) tended to be equal in size to the surrounding invasion nodes. Range shift publications shared a high number Wright et al.

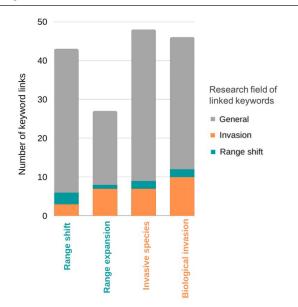


Figure 3. Total number of keyword links of the two most frequently occurring keywords from the field of range shift ecology ("range shift" and "range expansion", shown in teal) and invasion ecology ("invasive species" and "biological invasion", shown in orange). The colour of each bar represents the research field that each keyword is linked to (general = grey, invasion = orange, range shift = teal), with the size of each section representing the number of keyword links to those fields.

of links with both range shift and invasion publications in the network.

Citation networks

A variety of citation networks were constructed to investigate the relationship between rates of direct citation and number of citations publications have accrued.

Citation network A

Three citation networks were constructed using all range shift publications and randomly-selected invasion publications. For clarity only the first network is shown here (Fig. 5A; second and third networks shown in Appendix, Fig. S1 and Table S2.). The largest connected citation network consisted of 266 range shift publications and 638 invasion publications. There were 30 citation links in total between range shift and invasion publications. Range shift publications cited invasion publications approximately twice as often as vice versa range shift papers cited invasion publications cited range shift publications 16 times (0.025; Fig. 6).

Citation network B

The second citation network was constructed using all range shift publications and invasion publications

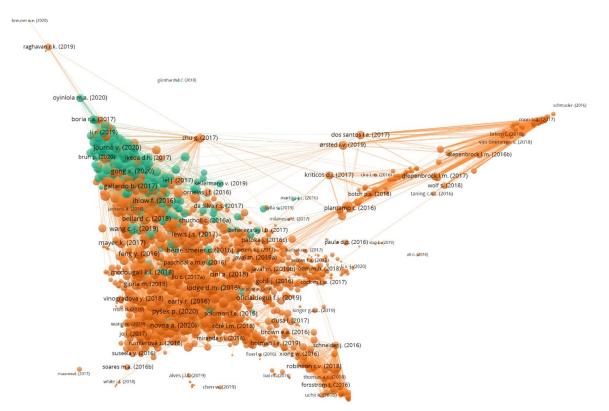


Figure 4. Bibliographic coupling network of range shift ecology (n = 260) and invasion ecology (n = 1540) publications published between 2016 and 2020. Nodes represent publications and are coloured based on research topic (teal = range shift ecology, orange = invasion ecology). Node size represents the number of links each publication has. Linking occurs when two publications both cite a third publication (links shown in grey to improve visualisation of node colour).

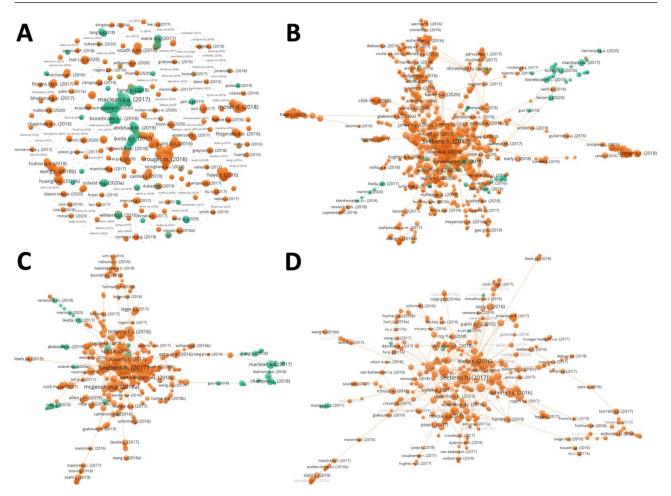


Figure 5. Largest connected citation networks of range shift ecology and invasion ecology literature published between 2016 and 2020. Publications are represented by nodes, which are coloured by research topic (teal = range shift, orange = invasion). A = All range shift ecology publications, and randomly selected invasion ecology publications; B = all range shift ecology publications, and invasion ecology publications with a minimum of 22 citations; C = all range shift ecology publications with a minimum of 30 citations; D = range shift ecology and invasion ecology publications with a minimum of 30 citations; D = range shift ecology and invasion ecology publications with a minimum of 30 citations are linked when a publication cites another. Node size represents the number of times a publication has been cited by another publication within the network (number of links). The distance between nodes indicates the relatedness of items, determined by the number of citations between publications. Note: link colour does not indicate citation direction.

with a minimum of 22 citations. The largest connected citation network consisted of 103 range shift publications and 801 invasion publications (Fig. 5B). There were 71 citation links between range shift and invasion publications. Range shift publications cited invasion publications about 20 times more frequently than vice versa – range shift papers cited invasion papers 50 times (leading to an average citation rate of 0.49 invasion publications cited per range shift paper), while invasion publications cited range shift publications 21 times (0.026 range shift publications cited per invasion paper; Fig. 6).

As this network had the highest number of direct citations between fields, a more in-depth examination of the publications in the network was undertaken. Invasion publications linked to range shift publications generally examined future climatedriven impacts of invasive species (Dainese et al. 2017, Wolf and Ripple 2017) or general meta analyses/literature review of invasion ecology (Early et al. 2016, Seebens et al. 2017). Range shift publications linked to invasion publications tended to discuss ecological niche modelling (Marzloff et al. 2016a, Ikeda et al. 2017, Ben Rais Lasram et al. 2020), present a meta-analysis/literature review describing trends or processes of range shifts (MacLean and Beissinger 2017, Guo et al. 2018, Lenoir et al. 2020), or examine range-shifting invasive species (Petitpierre et al. 2016, Wang et al. 2019, Rockwell-Postel et al. 2020). Age of publication did not appear to affect a publication's likelihood of being cited, with approximately half of all publications sampled per year linked via citation to another publication in the network.

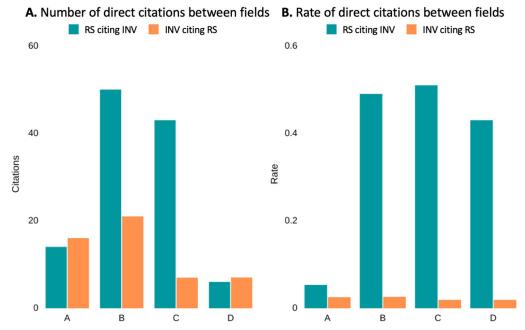


Figure 6. Number and rate of direct citations between range shift (RS) and invasion (INV) publications in citation networks A, B, C and D. Teal columns represent range shift publications citing invasion publications, and orange columns represent invasion publications citing range shift publications. A = All range shift ecology publications, and randomly selected invasion ecology publications; B = all range shift ecology publications, and invasion ecology publications with a minimum of 22 citations; C = all range shift ecology publications, and invasion ecology publications with a minimum of 30 citations; D = range shift ecology publications with a minimum of 30 citations.

Citation network C

The third citation network was made using all range shift publications, and invasion publications with a minimum of 30 citations. The largest connected network consisted of 85 range shift publications and 377 invasion publications (Fig. 5C). A total of 50 citation links between the two fields was observed. While far fewer range shift publications were included in the network, range shift publications cited invasion publications 43 times (rate = 0.51), which was more than an order of magnitude more frequently than invasion publications, rate = 0.019; Fig. 6).

Citation network D

The fourth citation network was formed from range shift and invasion publications with a minimum of 30 citations. The largest connected network consisted of 14 range shift ecology publications and 367 invasion ecology publications (Fig. 5D). Rates of citations between the two fields were very similar to the previous network (Fig. 6). Of the 13 total links between the two fields, range shift publications cited invasion publications six times (rate = 0.43) and invasion publications cited range shift publications seven times (rate = 0.019; Fig. 6).

When citations networks used randomly selected invasion publications, range shift papers recorded the lowest direct citation rate (0.053) (Fig. 6). In comparison, when only moderately and highly cited invasion publications (minimum 30 citations) were used, range shift papers were over ten times more likely to cite invasion publications (Fig. 6).

The rate at which invasion publications cited range shift publications remained very low across all networks, between 0.019 – 0.026 (Fig. 6).

Discussion

This study examined the level of cross-fertilisation and knowledge exchange between the research fields of range shift and invasion ecology, demonstrating that while the two fields are inherently strongly related, the level of exchange and integration does not reflect the conceptual closeness of the fields. Despite high potential, there appears to be a limited number of publications that draw upon research spanning both fields, with range shift publications more likely to integrate knowledge from invasion ecology than vice versa.

Both research areas demonstrated reasonably similar use of terminology. The clusters of keywords used by range shift and invasion fields were quite closely related (Fig. 1 and 2), consisting of terms common in biology and ecology rather than specific to specialised sub-fields. Additionally, a large number of links between range shift and invasion ecology publications occurred via bibliographic coupling (Fig. 4), suggesting that many range shift and invasion publications tend to cite papers with related themes. This association is likely due to both fields requiring similar background literature to support study

development (e.g., description of drivers that may lead to invasion or species redistribution like climate change; (Latombe et al. 2021) or specialised literature that may be used to explain similar observed patterns (e.g., concepts of range expansion are applicable to both fields). This hypothesis is supported by the citation analysis. Manual examination of the context for direct citations between range shift and invasion publications revealed that citations between the bodies of research tended to occur within the introduction section of respective papers. Furthermore, the range shift papers being cited by invasion publications tended to be those that had undertaken research into climate-driven movement of invasive species. Keyword co-occurrence examination also supports this hypothesis, as the term "climate change" appeared as the central theme for both fields and was the most frequently occurring keyword in the larger network (Fig. 2).

Considering the closeness of publication themes, it was surprising to see relatively few direct citations between the bodies of research in recent years (Fig. 5 and 6). Citation analysis suggested that range shift publications are more likely to directly cite invasion publications than the contrary. This trend was apparent throughout all citation analyses performed, with range shift papers citing invasion publications at least twice as frequently as vice versa (Fig. 6). Indeed, this result was evident even when assessing direct citation rates among range shift and invasion ecology publications that were shown to be bibliographically coupled and linked by publication theme (green 'climate change' cluster, Fig. S2 and S3). Among these papers, there remained an imbalance in numbers of citations, with range shift publications citing invasion publications more frequently (Table S3). Our comparison of results across different levels of citations and using random draws of invasion papers suggests that this imbalance is not solely driven by the high number of invasion publications analysed relative to the number of range shift papers. Although range shift papers cite invasion papers more often than vice versa, the citation rate is generally quite low for both. Thus, there are likely a number of barriers limiting the potential for reciprocal exchange between the fields.

Barriers to knowledge exchange

Despite studying many similar phenomena, a key difference between range shift and invasion ecology lies in the research perspective of each field. This difference was made evident within the keyword cooccurrence network, with invasion publications using a variety of keywords relating to the management of invasion impacts (e.g., biological control, risk assessment, eradication), and range shift publications using keywords targeting mechanisms of species shifts (e.g., functional traits, biotic interactions, habitat fragmentation). Invasion ecology, being primarily concerned with mitigating the negative impacts of invasive species on recipient communities (Wallingford et al. 2020), is generally focussed on the regulation, management and prevention of biological invasions (Brown and Barney 2021). Much of the work

in invasion ecology has therefore been concentrated on identifying, characterising, and limiting the spread of invasive species (Richardson and Pyšek 2007, Brown and Barney 2021). However, viewing invasions in isolation and overlooking the community context within which invasions occur risks misconstruing the many factors that dictate invasion success and resulting community impacts (Pearson et al. 2018, Brown and Barney 2021). The invader-focused perspective may limit the mechanistic understanding of invasive processes and ecosystem effects, potentially restricting its applicability within other ecological fields. Hence, more remains to be done to create a shared research perspective that fosters integration between range shift and invasion ecology.

Opposing connotations

Divergent research perspectives may also result from the development of shared terms with opposing connotations, which could hinder efforts to integrate knowledge from the two fields. This is evident when considering habitat refuges or stepping stones, which are small areas or patches of habitat that allow species to expand their range through unfavourable or uninhabitable areas by providing refuge from suboptimal conditions (Cannizzo and Griffen 2019, Cannizzo et al. 2020, Gauff et al. 2023). These refuges can be formed naturally (e.g., forest fragments), or artificially, as is the case for artificial reefs (Sheehy and Vik 2010). While artificial habitats have been shown to facilitate movement of species at their range edges (Cannizzo and Griffen 2019, Paxton et al. 2019), they also facilitate invasions (Bulleri and Airoldi 2005, Glasby et al. 2007, Vaselli et al. 2008, Airoldi et al. 2015), through association with human activities (e.g. shipping) (Hewitt et al. 2004, Glasby et al. 2007), provision of substrate on which invasive species can become established (Glasby et al. 2007, Komyakova et al. 2022), or similarity to the invader's native habitat (Davis et al. 2014). Thus, while habitat refuges such as artificial reefs are seen to be beneficial from the perspective of range shifts, they are viewed negatively from an invasion standpoint. Publications will therefore likely offer opposing conclusions and recommendations regarding management and conservation of new species inhabiting these areas, which in some contexts may limit the utility of research exchange. However, as range shifts and invasions are both mediated by stepping-stones, it is vital that both perspectives are considered within the framework of changing community composition. Despite differences in perspective, there is still much that each body of research can learn from the other in the context of ecological processes.

Methods and distance of species dispersal

Another key difference between range shifts and invasions that could limit how readily theories and findings can be exchanged relates to the method and distance of species dispersal. Invasion ecology implies assisted movement far outside a species' native range due to human intervention, whereas

range shifts involve dispersal from a species' native range into adjacent regions made habitable by climate change, without direct human assistance (Urban 2020). How spatially distant donor communities are to recipient communities will influence the level of shared evolutionary history between them, and thus vary the potential impact shifting species have on recipient communities (Urban 2020). Species originating from adjacent communities, such as those undergoing climate-driven redistribution, are likely to share evolutionary history with recipient communities, which may reduce the potential for negative community impacts (Wallingford et al. 2020). Invasive species largely originate from distant communities and are unlikely to share evolutionary history, increasing the likelihood for negative impacts to recipient communities (Urban 2020). This key difference between range shift and invasion ecology could discourage comparisons and make it less likely that knowledge from one field is applied to the other.

Age and size of research fields

A possible cause of the poor level of integration observed between research fields relates to the age of each field and, by extension, different rates of publication. Invasion ecology has received more than half a century of dedicated research (e.g., since Elton 1958), whereas range shifts have been studied for less than half that period (an early seminal paper being Southward, Hawkins & Burrows 1995). This unevenness is reflected in the number of publications returned within the systematic literature review for each field. This asymmetry affected our ability to analyse the level of exchange between the two fields.

The large volume of invasion literature being generated each year may pose an unexpected barrier to reciprocal exchange with range shifts. It is possible that authors in large fields such as invasion ecology find it challenging to remain up-to-date and cognisant of all emerging research within their own field (Chu and Evans 2021). As a result, their ability to also stay well-informed of research within other related areas is diminished. Furthermore, if arrival rate of new ideas (for example, integration of range shift concepts within invasion ecology) is too fast, competition with established ideas may prevent novel concepts from becoming known and accepted within the field (Chu and Evans 2021). This could lead to a trend of "benign neglect" (Menge et al. 2009), whereby invasion researchers have a reduced ability to study range shift papers. In comparison, the extent of range shift research is more limited and thus may compel researchers to expand their research horizons and utilise invasion literature more often. This hypothesis would be supported by our finding that range shift papers tend to reference invasion papers more often than vice versa. In addition, invasion ecology has developed independently of range shift ecology. Historical influences, including the trend of mono-disciplinary studies (see Hof 2021), have likely combined with the factors discussed previously, making it less likely for invasion publications to cite range shift

literature. Therefore, limited communication and other barriers mean data and findings are not disseminated beyond research fields, and thus theories developed in one area may not be considered more broadly (Twiname et al. 2020).

Benefits of reciprocal exchange

The need for increased knowledge exchange between related ecological fields is becoming more urgent as climate-change effects worsen (IPCC 2021). Climate-driven species redistribution is pervasive and accelerating, yet the mechanisms remain poorly understood (Twiname et al. 2020). Reciprocal exchange has the potential to allow more rapid dissemination of data, hypotheses and concepts and reduce the probability of duplicated research, thereby saving time. Techniques and methods (e.g., detection or modelling) developed in one field may also be used across multiple fields. Researchers are beginning to appreciate the value of incorporating invasion ecology concepts into range shift research.

Within the last decade, a small number of publications utilising invasive risk assessment frameworks within the context of species redistributions have emerged (Gilman et al. 2010, Wallingford et al. 2020, Henry and Sorte 2022). Invasion frameworks have been developed to assess potential impacts of invasive species on communities and ecosystems. In the context of climate-driven range shifts, they can be used in a variety of ways. Considering species redistribution from the perspective of invasion ecology can improve our understanding of and ability to predict impacts of climate-driven range shifts and provide tools for formal assessment of risks to community structure and function (Sorte et al. 2010, Robinson et al. 2015). Climate-driven range expansions are similar to species invasions (Sorte et al. 2010, Bates et al. 2013), meaning that invasion frameworks can be adapted to identify characteristics of species undergoing range extensions that are shared with high-impact invasive introductions, providing insight into how to consider novel interactions and assess high and low risk species on a case-by-case basis. This is possible because, despite certain known differences between invasive species and range shifting species (such as degree of shared evolutionary history with recipient ecosystem), climate-driven impacts and invasive impacts can occur through analogous mechanisms and become more likely when there are cases of wide dispersal, community disturbance, low biotic resistance (Bates et al. 2014, Wallingford et al. 2020) and 'invasional meltdown' (Bates et al. 2017, Ling et al. 2018). For example, 'invasion syndromes', which have been proposed as a way of predicting and managing biological invasions (Novoa et al. 2020), are a promising area of research that could be easily adapted for use within range shift ecology. Invasion syndromes are defined as "a combination of pathways, alien species traits, and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions"

(Novoa et al. 2020). Identifying similar 'syndromes' within a range shift context could be beneficial in identifying similarities between redistribution events while accounting for context-dependency, as well as developing transferrable risk assessment and management procedures (Novoa et al. 2020).

A topic of concern within invasion ecology is the effect of climate change on biological invasions (Hellmann et al. 2008, Robinson et al. 2020). Climatedriven alterations to invasive vectors, pathways, and abiotic and biotic interactions in recipient communities are likely to affect establishment success and spread of invasive species (Mahanes and Sorte 2019, Robinson et al. 2020). Predicting the ecological consequences of climate change for species invasions requires a sound understanding of ecosystem processes and dynamics. To date, range shift and invasion fields have taken different routes when modelling potential species impacts, to varying degrees of success. Invasion science has typically invoked fewer processes, focussing instead on the interaction between invader and novel abiotic and biotic environment (Latombe et al. 2021), whereas range shift biologists tend to invoke a combination of processes across multiple levels (Twiname et al. 2020, Latombe et al. 2021). As changes in climate will affect the performance and success of both invasive and native species (Robinson et al. 2020), impacts to recipient communities will be a result of both direct and indirect effects of climate change. The pervasive nature of range shifts makes it likely that communities experiencing species invasion will also be experiencing a redistribution of species. Indeed, the cumulative effect of multiple species shifts can have significant negative impacts on ecosystem dynamics and productivity (Marzloff et al. 2016b). The combined ecological effects of species range shifts and species invasions on ecosystem structure and functioning, as well as to human systems, could be substantial (Bradley et al. 2022). However, impacts are difficult to anticipate and manage, requiring wholeof-ecosystem monitoring and management to limit the potential for negative effects of species invasions and simultaneous range shifts (Marzloff et al. 2016b). Therefore, integrating range shift knowledge into invasion practice and theory (and vice versa) has the potential to improve the predictive capacity of models and better inform management and conservation (Nackley et al. 2017, Doherty et al. 2023). For example, Van Kleunen et al. (2023) have proposed a framework for assessing risk and aiding decision-making for species introductions that requires users to forecast of addition of new species, their interaction, and predicted consequences to ecosystems, which allows managers to evaluate possible outcomes and tradeoffs in uncertain scenarios.

Limitations to bibliometric analysis

Due to the ever-increasing volume of ecological literature being published, there is growing demand for software tools that can be used to perform literature review analysis and bibliometrics to visualise trends, emerging themes, and gaps in research. Tools such as VOSviewer (van Eck and Waltman 2010) and the bibliometrix R package (Aria and Cuccurullo 2017) are optimised for constructing and visualising bibliometric networks from large amounts of complex data; however, there are limitations to the depth of analysis permitted. Loss of information occurs when reducing bibliographic data into a network, as well as during the visualisation of the bibliographic network (Van Eck and Waltman 2014). For instance, when constructing a citation network, the analysis does not show the context in which the citation is used, which requires manual examination of publications. Similarly, bibliographic coupling networks do not provide information about the specific references shared by two papers, beyond the number of shared references ("link strength"). Furthermore, displaying the position of nodes in a two-dimensional space does not reflect the true relatedness of nodes, and therefore distance provides only an approximation of relatedness (Van Eck and Waltman 2014). Unfortunately, the bibliometric software used within this study (limited to approximately 2000 papers per network) was unable to process the extremely large amounts of invasion ecology data, which resulted in the need to subsample references from the total literature on the topic. Although, to some degree, subsampling was desirable to better balance sample size differences between the range shift and invasion literature, this limitation could constrain the accuracy of bibliometric analysis. Thus, the software tools used are not yet optimised for analysis of knowledge exchange between all research fields, particularly those with large amounts of literature. Until software is developed that allows greater depth of analysis, these bibliometric tools can only offer an initial probe into potential trends, as further examination of the mechanisms behind trends currently requires manual investigation.

Future applications

This study can be considered as a first step in recognising the need for increased knowledge exchange between range shift and invasion ecology. Both fields would benefit from further research into potential barriers that may be limiting reciprocal exchange of theories, concepts, frameworks and ideas. Applying principles of co-design (e.g., sharing knowledge through networks and mentorship, providing cross-boundary training and opportunities, and incentivising and celebrating knowledge codesign) (Satterthwaite et al. 2022), will facilitate the dissemination and use of available knowledge (Pecl et al. 2022), allowing scientists and decisionmakers to develop innovative policies and solutions that optimise environmental benefit (or at the very least, minimise harm).

There is great potential for the results of this study to contribute towards the synthesis of a map of terms and concepts used within invasion and range shift fields (Enders et al. 2018, Enders et al. 2020), which would reveal the similarity and differences between hypotheses. The methods employed here could be used as a basis for a bibliographic approach when developing a network of hypotheses (i.e., two hypotheses are connected if publications featuring each hypothesis are frequently cited together) (Enders et al. 2019). Assessing the conceptual similarity of range shift and invasion hypotheses would allow researchers to navigate the overlap (and any possible contradiction) within concepts and theories of the two research areas, as well as determine which factors are considered most important for successful species shifts and invasions (Enders et al. 2019). A map of common terms would also be useful in the context of meta-analyses, to ensure that researchers consider the broad range of terminology used within ecological fields (Orr et al. 2020).

The similarities between these two research fields presents an ideal opportunity to combine information and methods into a comprehensive predictive framework, that integrates factors influencing the ecological impacts of both range shifting species and invasive species (Bonebrake et al. 2018, Twiname et al. 2020). Developing and expanding theoretical and predictive frameworks would support mechanistic understanding and modelling of species movements under climate change. An integrated predictive framework that incorporates information from both fields would be highly beneficial from a conservation and management standpoint. Ultimately, this will require improved data sharing and assimilation to link ecological processes across scales and gradients (Bradley et al. 2022), using statistical modelling approaches that incorporate multiple data sources within a unified analytical framework (Zipkin et al. 2021). Data integration such as this could be used within ecology to expand the scope of research and conclusions, increase understanding of mechanistic processes and precision of predictions, and account for multiple sources of uncertainty in model parameters (Zipkin et al. 2021). Adopting modelling approaches that incorporate multiple data sources within an analytical framework could be particularly useful for understanding mechanistic processes, which require integration of different datasets (Ibáñez et al. 2014, Levy et al. 2014, LaRue et al. 2021).

Conclusions

Results of this study demonstrate that the current degree of cross-fertilisation between range shift ecology and invasion ecology is low, despite the two fields being strongly linked in terms of concepts and processes. Now, more than ever, there is an increasing need to move away from discipline-focused interpretation and communication of results, towards greater research integration and connection between related ecological fields (Macdonald et al. 2018). In the context of current and future global change, both range shifting species and invasive species have the potential to alter the structure and functioning of ecological systems (Pyšek and Richardson 2010, Pecl et al. 2017). Adopting bi-directional exchange between range shift and invasion ecology would promote the development of a unified research framework, which could improve predictions of species movements,

impacts and ecosystem responses to related stressors, thereby offering potential for improving conservation and management strategies (Macdonald et al. 2018, Twiname et al. 2020). Improved communication within related ecological fields is vital, not only from the perspective of biodiversity conservation, but to ensure the protection of ecosystem services and human systems in the face of a rapidly changing global climate.

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Author contributions

BW: Conceptualisation, Methodology, Data curation, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. VK: Conceptualisation, Writing – review & editing. CS: Conceptualisation, Writing – review & editing. MT: Conceptualisation, Methodology, Writing – review & editing. GP: Conceptualisation, Writing – review & editing.

Data Accessibility Statement

R code and bibliographic data used in our analyses are available at https://metadata.imas.utas. edu.au/geonetwork/srv/eng/catalog.search#/ metadata/5185db15-056a-462c-a31a-3837f1933f4b.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Figure S1. Citation networks of range shift ecology and randomly selected invasion ecology publications. **Figure S2**. Bibliographic coupling network coloured by publication theme.

Figure S3. Citation network of thematically linked publications from Fig. S2.

Table S1. List of author keywords replaced by a shortened form during keyword co-occurrence analysis.

Table S2. Number and rate of direct citations frompublications in Fig. S1.

Table S3. Number and rate of direct citations frompublications in Fig. S3.

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