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REVIEW AND SYNTHESIS

A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits

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Abstract

Global change has made it important to understand the factors that shape species' distributions. Central to this area of research is the question of whether species' range limits primarily reflect the distribution of suitable habitat (i.e. niche limits) or arise as a result of dispersal limitation. Over-the-edge transplant experiments and ecological niche models are commonly used to address this question, yet few studies have taken advantage of a combined approach for inferring the causes of range limits. Here, we synthesise results from existing transplant experiments with new information on the predicted suitability of sites based on niche models. We found that individual performance and habitat suitability independently decline beyond range limits across multiple species. Furthermore, inferences from transplant experiments and niche models were generally concordant within species, with 31 out of 40 cases fully supporting the hypothesis that range limits are niche limits. These results suggest that range limits are often niche limits and that the factors constraining species' ranges operate at scales detectable by both transplant experiments and niche models. In light of these findings, we outline an integrative framework for addressing the causes of range limits in individual species.

Keywords

Abiotic constraints, climate, dispersal limitation, fitness, geographical distribution, over the edge transplant, species distribution modelling.

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INTRODUCTION

Explaining species' geographical range limits is an outstanding challenge for evolutionary ecologists and has become of imminent importance as we strive to predict the consequences of environmental change on biodiversity. Central to this area of research is the question of whether observed range limits coincide with the limits of species' ecological niches (Gaston 2003; Sexton *et al.* 2009; Peterson *et al.* 2011) – that is whether range limits are primarily set by the availability of suitable abiotic and biotic conditions, or better reflect constraints on dispersal. Addressing this question reveals the relative importance of different ecological processes shaping species' distributions and provides insight into the type of traits that limit range expansion, thus paving the way for more mechanistic studies of range limits.

Over-the-edge transplant experiments (TEs) have been hailed as the gold standard for testing the importance of niche constraints on range limits (Gaston 2003). These experiments directly assess the ability of individuals to survive and reproduce when moved beyond the range, with the expectation that fitness will be lower at sites beyond the range than within the range if range limits are niche limits. A recent survey of existing TEs found support for this prediction in the majority of published studies and concluded that range limits are commonly associated with niche constraints (Hargreaves *et al.* 2014). However, TEs are not practical for many taxa, limiting the generalities that can be made from these studies. Furthermore, TEs are difficult to conduct with the level of replication and over the timeframes necessary to fully evaluate potential persistence beyond the range. Thus, the results from TEs are difficult to extrapolate to spatial and temporal scales relevant to range dynamics.

Ecological niche models (ENMs) have emerged as an additional means for addressing whether range limits are niche limits (e.g. Anderson *et al.* 2002; Morin *et al.* 2007; Graham *et al.* 2010; Bulgarella *et al.* 2014). Such models are generated from freely available GIS data sets and species occurrence records and are thus a feasible alternative to TEs for many species. These models also have the advantage of allowing investigators to quickly generate predictions about suitable habitat across entire landscapes and, because the variables considered are often summaries of conditions across multiple years, to address niche limits over longer timeframes. However, there are different perspectives as to how best to generate ENMs (Araújo & New 2007; Royle *et al.*

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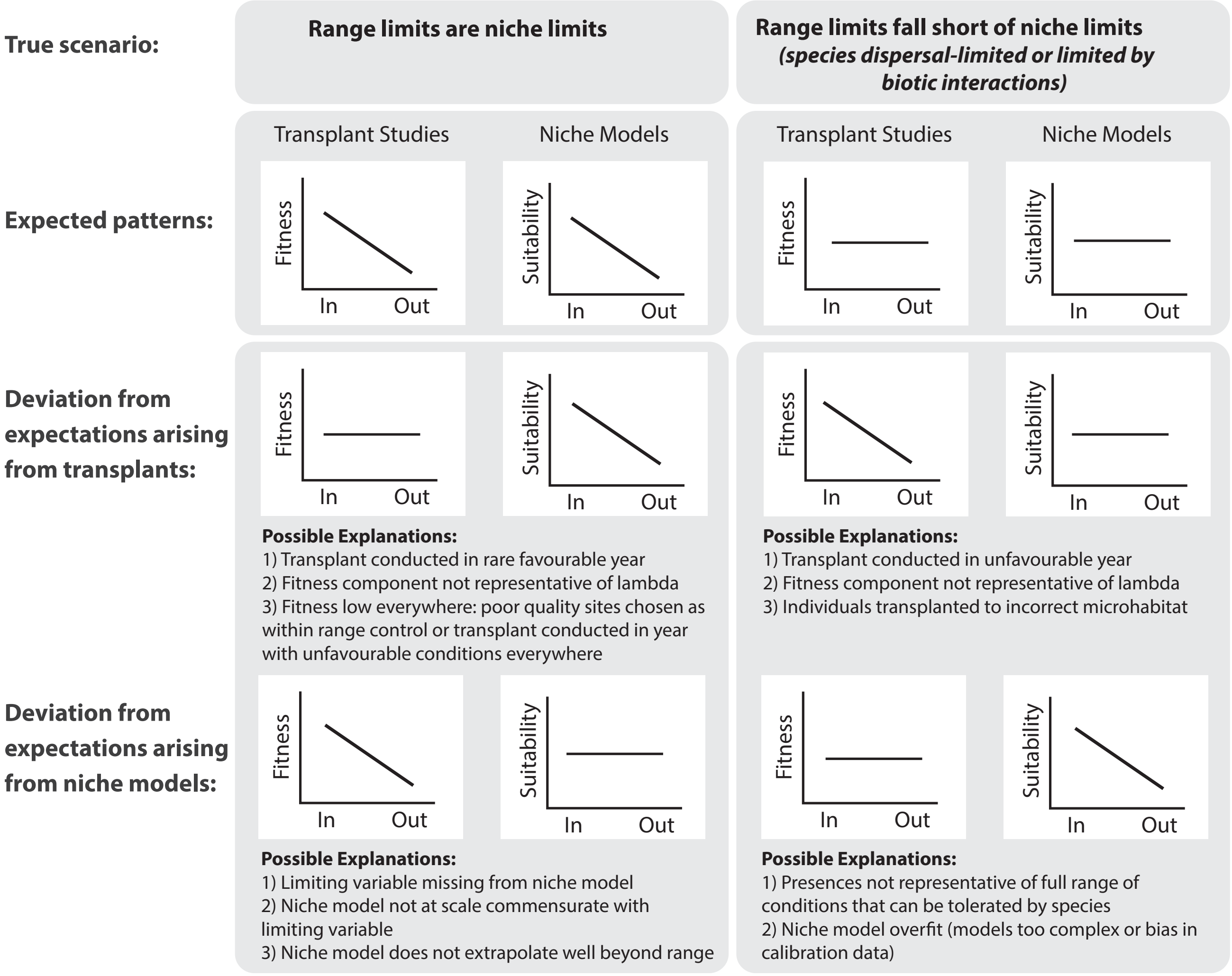
2012; Merow *et al.* 2013). Furthermore, independent data for validating model predictions are usually lacking and problems with existing evaluation metrics (e.g. Lobo *et al.* 2008; Veloz 2009; Jiménez-Valverde 2012) make it difficult to gauge the performance of ENMs, particularly in regions (or time periods) that differ from those considered during model calibration.

In theory, both a well-designed TE and an accurate ENM should yield congruent inferences as to whether range limits correspond with niche limits. Thus, comparing the inferences from both approaches serves as a means for validating conclusions about the causes of range limits. For a given species, we expect both the fitness of transplanted individuals and the suitability of sites inferred from ENMs to decline across range limits if range limits are niche limits, and both to remain high if species are dispersal limited (Fig. 1). Across species, evaluating the frequency of cases fully supporting either hypothesis overcomes any issues with individual TEs or ENMs (e.g. Fig. 1) and provides an even stronger test of the alternative hypotheses for range limits than comparative studies based on either method alone (e.g. Hargreaves *et al.* 2014; Cunningham *et al.* 2016).

However, there is an additional reason why a comparison of results from TEs and ENMs across species should be informative. The differences in scale at which TEs and ENMs are often conducted may mean that the two methods capture different aspects of the niche. ENMs, when calibrated from coarse-scale data sets (e.g. the 1 km resolution of the commonly used WorldClim layers from Hijmans *et al.* 2005), are more likely to capture processes operating at broad spatial scales than at fine scales (e.g. Peterson *et al.* 2011), whereas the results of TEs may additionally reflect local conditions and biotic interactions. Assessing the extent of concordance between TEs and ENMs thus speaks to the overall importance of processes operating at different scales for range limits.



Possible Explanations:
1) Transplant conducted in rare favourable year
2) Fitness component not representative of lambda
3) Fitness low everywhere: poor quality sites chosen as within range control or transplant conducted in year with unfavourable conditions everywhere

Possible Explanations:
1) Transplant conducted in unfavourable year
2) Fitness component not representative of lambda
3) Individuals transplanted to incorrect microhabitat

Possible Explanations:
1) Limiting variable missing from niche model
2) Niche model not at scale commensurate with limiting variable
3) Niche model does not extrapolate well beyond range

Possible Explanations:
1) Presences not representative of full range of conditions that can be tolerated by species
2) Niche model overfit (models too complex or bias in calibration data)

Fig. 1 Inferences about the causes of species' geographical range limits from the combination of over-the-edge transplant studies and ecological niche models. Top panels show the expected results from both types of studies under alternative scenarios whereby a species is or is not niche limited. Panels below highlight the potential ways in which the conclusions from transplant studies and niche models can differ, with possible explanations for the discordance. For simplicity, the potential for fitness (or suitability) to increase beyond range limits is not shown but we note that such a scenario could potentially arise if natural enemies prevent species from occupying optimal habitat.

In this study, we gathered published over-the-edge transplant results from 40 species. Using common sources of spatial data (i.e. the Global Biodiversity Information Facility for locality data and the BIOCLIM database [Hijmans *et al.* 2005;]) and the widely employed niche modelling software, MAXENT (Phillips *et al.* 2006), we built ENMs for each of these species and asked: (1) Does the predicted suitability of sites (like the fitness of individuals at sites: Hargreaves *et al.* 2014) decline across range limits, as expected if range limits are niche limits? and (2) Within species, are the results from TEs and ENMs concordant? Our results revealed declines in both fitness and suitability across range limits for most species, providing strong support for the hypothesis that range limits are often associated with niche limits. Apart from shedding light on the processes shaping species' distributions, these findings have implications for the empirical evaluation of range limits in a broad array of organisms and we end by offering some suggestions in this regard.

MATERIALS AND METHODS

Transplant data

We searched the ISI Web of Science and Google Scholar at the end of 2012 for studies conducting TEs with terrestrial species (search terms were 'transplant' or 'translocat*' combined with 'distribution' or 'range' and 'limit' or 'boundar*' or 'edge'; papers cited by or citing returned papers were also considered). For inclusion in our final data set, species had to have been transplanted beyond either a latitudinal or longitudinal (hereafter 'horizontal') or elevational (hereafter 'vertical') range limit on their native continent (over-edge sites), as well as to one or more in-range control sites. Authors of the TE studies used various methods to determine the location of the range edge, including surveys (12 species), mapping collection records (8 species), coincidence with major plant community shifts (3 species) and previously published studies and floras (17 species; Table S1-1). We relied on the designations made by the authors to classify the position of TE sites with respect to the range edge. Studies that did not provide site-specific performance and/or geographical coordinates were excluded unless this information was available upon contacting the original authors or could be obtained from figures (performance data extracted using DataThief [Tummers 2006]; site coordinates georeferenced in GoogleEarth). Five species were discarded due to a lack of available locality data for building ENMs (below), producing a final data set of 40 species from 24 published studies (Table 1).

We recorded the mean performance of individuals per site, relying on the best fitness proxy published for each species according to the following hierarchy: lifetime fitness (average lifetime reproduction per individual) was used over integrated fitness (survival × reproduction) was used over reproduction (e.g. fruits per plant or eggs per individual) was used over survival (proportion of individuals surviving to reproduction or, in the case of perennial plants, proportion of individuals surviving to end of experiment). In cases where the effects of different treatments (e.g. fertilising) on transplant success were tested, we used data from the treatment that best approximated conditions that would be experienced by individuals dispersing unassisted. For four species, estimates of fitness were provided for multiple life stages but the study design precluded us from calculating an average or a cumulative value across life stages. For two of these species, we used data from the life-history stage for which the best fitness proxy (according to the above hierarchy) was reported. For the other two species, along with five species reporting results for a single life-history stage, the TE was replicated across multiple years. For these species, we used data from the first replicate that provided the best fitness data for the greatest number of sites (selecting alternative replicates did not affect our final results). Finally, five species had multiple transplant sites occurring in the same grid cell in the raster layers used to generate the ENMs (see below). To avoid non-independence imposed by the resolution of the raster data, we retained only one site, chosen at random, from each set of cell duplicates (except in two cases where an in-range and over-the-edge site occurred in the same cell, in which case both were removed from the final data set). All data reported as log-transformed values in the original studies were back-transformed prior to standardisation and further analysis.

Niche models

Locality data for each species were obtained from the Global Biodiversity Information Facility (GBIF; accessed up to October 2013). Records from continents where species are non-native, or that had low coordinate precision (e.g. fewer than two decimal places included in GPS coordinates), or that were based on fossil or cultivated specimens were excluded. Locality data sets with < 30 records were supplemented with records from other sources where possible. The final number of records per species ranged from 12 to 24 495 (Table 1).

ENMs were built using MAXENT (version 3.3.3; Phillips *et al.* 2006) as executed in the *dismo* package (Hijmans *et al.* 2013) in R (version 3.0.3 and 3.2.2). Models were based on the 19 BIOCLIM layers available from the Worldclim website (http://www.worldclim.org/bioclim; Hijmans *et al.* 2005), downloaded at 1 km resolution and projected to an equal area projection. Raster data were processed in the *raster* package (Hijmans & van Etten 2012) in R. To avoid over-parameterisation and reduce correlations among variables, the BIOCLIM variables were summarised for each species using principal components analysis (PCA). These species-specific PCAs were based on 5000 randomly selected points from within a rectangular extent bounding the locality data and the first six principal components were used to generate the ENM for each species (these axes explained 96.5–99.7% of the total variance in climatic conditions across the area occupied by each species). Thirteen species had a limited number of locality records (Table 1) and further variable reduction was considered optimal (e.g. Harrell *et al.* 1984). For these species, models were rerun, retaining only the three principal components that made the largest contributions to the initial six-variable niche model. For most species, models were built using hinge features, which accommodate both linear and threshold-like

Table 1 Summary of transplant experiments (TEs) and niche models (ENMs) used to determine whether fitness and suitability decline (−) or not (+) across range limits

Species	Taxonomic group	Source of TE data	Type of range limit*	Best fitness proxy[†]	Life stage[‡]	TE length (years)	Num TE sites (in/out)	Range size (m^2)	Num Locs ENM	Mean AUC ENM	Pattern (fitness/suitability)[¶¶]
Abutilon theophrasti	Plant (annual)	Andersen *et al.* 1985	H	S × R	1	1	3 (1/2)	9.38×10^{12}	276	0.90	−/−
Acer saccharum	Plant (tree/shrub)	Kellman 2004	H	S	1	7	2 (1/1)	6.39×10^{12}	404	0.85	−/−
Anelosimus baeza	Animal (arachnid)	Purcell & Aviles 2008	V	S	3	1	3 (2/1)	4.67×10^{12}	19	0.86[§]	−/−
Aphragmus oxycarpus	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (1/3)	2.47×10^{12}	97	0.81	−/−
Arnica montana	Plant (herb. perennial)	Bruelheide & Scheidel 1999	V	S	3	1	3 (1/2)	3.93×10^{12}	13233	0.93	−/−
Atalopedes campestris	Animal (insect)	Crozier 2004	H	S × R	1	1	2 (1/1)	1.23×10^{13}	69	0.73[¶]	−/−
Betula papyrifera	Plant (tree/shrub)	Hobbie & Chapin 1998	H	S	2	3	2 (1/1)	1.44×10^{13}	648	0.85	−/−
Camissoniopsis cheiranthifolia[**]	Plant (herb. perennial)	Samis & Eckert 2009	H	LTF	2	3	5 (4/1)	2.95×10^{11}	26	1.00[¶]	−/+
Chamaecrista fasciculata[††]	Plant (annual)	Stanton-Geddes *et al.* 2012	H	LTF	1	1	5 (3/2)	8.64×10^{12}	438	0.87	−/−
Clarkia xantiana ssp. parviflora[‡‡]	Plant (annual)	Geber & Eckhart 2005	H	LTF	1	1	3 (2/1)	1.23×10^{10}	29	0.90[¶]	−/−
Clarkia xantiana ssp. xantiana[‡‡]	Plant (annual)	Geber & Eckhart 2005	H	LTF	1	1	3 (2/1)	2.83×10^{10}	12	0.80[§]	−/−
Digitalis purpurea	Plant (biennial)	Bruelheide & Heinemeyer 2002	Both	S	2	1	9 (7/2)	5.65×10^{12}	22225	0.83	−/−
Draba altaica	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (2/2)	2.48×10^{12}	193	0.81	−/−
Draba oreades	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (2/2)	2.17×10^{12}	129	0.81	−/−
Euphorbia amygdaloides	Plant (evergreen perennial)	Schulz & Bruelheide 1999	H	S	3	1	8 (4/4)	5.23×10^{12}	8568	0.89	+/−
Gilia capitata ssp. capitata	Plant (annual)	Nagy & Rice 1997	H	S × R	1	1	2 (1/1)	1.11×10^{12}	398	0.89	−/−
Hordeum murinum	Plant (annual)	Davison 1977	V	R	1	1	3 (1/2)	2.23×10^{13}	18019	0.96	−/−
Lactuca serriola	Plant (annual)	Prince & Carter 1985	H	S × R	2	1	5 (2/3)	2.37×10^{13}	19335	0.96	+/−
Lipoptena cervi	Animal (insect)	*Härkönen et al.* 2010	H	S	2	1	5 (2/3)	2.71×10^{12}	278	0.87	−/−
Lomatium dissectum var. dissectum	Plant (herb. perennial)	Marsico & Hellmann 2009	H	S	1	2	2 (1/1)	2.06×10^{12}	267	0.77	−/−
Lomatium nudicaule	Plant (herb. perennial)	Marsico & Hellmann 2009	H	S	1	2	2 (1/1)	8.00×10^{11}	206	0.84	+/−
Lomatium utricularium	Plant (herb. perennial)	Marsico & Hellmann 2009	H	S	1	2	2 (1/1)	5.41×10^{11}	145	0.85	−/−
Mimulus cardinalis	Plant (herb. perennial)	Angert & Schemske 2005	V	S × R	2	3	4 (2/2)	1.59×10^{12}	523	0.89	−/−
Mimulus lewisii	Plant (herb. perennial)	Angert & Schemske 2005	V	S × R	2	3	4 (3/1)	1.39×10^{12}	210	0.91	−/−
Mnium arizonicum	Plant (bryophyte)	Cleavitt 2004	V	S	2	1	9 (5/4)	2.57×10^{12}	22	0.91[§]	+/−
Mnium spinulosum	Plant (bryophyte)	Cleavitt 2004	V	S	2	1	9 (4/5)	8.61×10^{12}	111	0.87	+/−
Pegaeophyton scapiflorum	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (1/3)	2.04×10^{12}	49	0.76[¶]	−/−

(continued)

Table 1. (continued)

Species	Taxonomic group	Source of TE data	Type of range limit[*]	Best fitness proxy[†]	Life stage[‡]	TE length (years)	Num TE sites (in/out)	Range size (m^2)	Num Locs ENM	Mean AUC ENM	Pattern (fitness/ suitability)[¶¶]
Phlox drummondii[‡‡]	Plant (annual)	Levin & Clay 1984	H	LTF	1	1	9 (5/4)	3.43×10^{12}	22	0.77[§]	−/−
Picea glauca	Plant (tree/ shrub)	Hobbie & Chapin 1998	H	S	2	3	2 (1/1)	1.77×10^{13}	368	0.81	−/−
Pinus albicaulis	Plant (tree/ shrub)	McLane & Aitken 2012	H	S	1	3	10 (4/6)	1.56×10^{12}	112	0.88	+/−
Poa attenuata	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (1/3)	6.60×10^{12}	459	0.91	−/−
Populus tremuloides	Plant (tree/ shrub)	Hobbie & Chapin 1998	H	S	2	3	2 (1/1)	2.02×10^{13}	700	0.86	−/−
Protea aurea	Plant (tree/ shrub)	Latimer *et al.* 2009	Both	S	2	2	5 (1/4)	1.96×10^{11}	30	0.98[¶]	−/−
Protea mundii	Plant (tree/ shrub)	Latimer *et al.* 2009	H	S	2	2	5 (1/4)	3.04×10^{11}	37	0.81[¶]	−/−
Protea punctata	Plant (tree/ shrub)	Latimer *et al.* 2009	Both	S	2	2	5 (2/3)	2.11×10^{11}	50	0.91[¶]	−/−
Saxifraga nanella	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S×R	3	2	4 (2/2)	1.04×10^{12}	34	0.95[¶]	−/−
Stellaria depressa	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (1/3)	1.55×10^{11}	119	0.98	−/−
Thaumetopoea pityocampa	Animal (insect)	Battisti *et al.* 2005	Both	S	1	1	9 (6/3)	1.38×10^{12}	38	0.83[¶]	−/−
Vulpia fasciculata[§§]	Plant (annual)	Norton *et al.* 2005	H	LTF	1	4	13 (8/5)	3.84×10^{12}	220	0.93	+/−
Waldheimia tridactylites	Plant (herb. perennial)	Klimeš & Dolezal 2010	V	S × R	3	2	4 (3/1)	1.11×10^{12}	135	0.95	+/−

[*] V = elevational; H = horizontal.
[†] S = survival; R = reproduction; S × R = survival × reproduction; LTF = lifetime fitness.
[‡] 1 = seeds or eggs; 2 = seedlings, juveniles or pupae; 3 = adults.
[§] 3 PCs used; models evaluated by comparing AUC to null distribution.
[¶] 3 PCs used.
[**] Relative fitness declined across range limit; absolute fitness > 1 inside and outside of range.
[††] Relative fitness declined across range limit; absolute fitness < 1 inside and outside of range.
[‡‡] Relative fitness declined across range limit; absolute fitness > 1 inside the range and < 1 outside of range.
[§§] Relative fitness did not decline across range limit; absolute fitness > 1 inside and outside of range.
[¶¶] Results shown are based on the analysis of all species, regardless of range limit type (V and H).

relationships and tend to be more GAM-like (Phillips & Dudík 2008; Elith *et al.* 2011). For four species, the number of unique locality records was small (< 25) and models were based on linear features alone. The maximum number of iterations in Maxent was set to 5000 to ensure model convergence. All other parameters were left at default values.

To approximate areas that the species could have reasonably 'sampled' over the course of establishing its range and thus to avoid the assumption that species are at equilibrium with respect to climate (see Discussion in Phillips 2008), we restricted background points for model calibration to the minimum convex polygon (MCP) around the locality data for each species. MCPs were generated using the *adehabitatHR* package (Calenge 2006) in R. We note that extrapolation to environmental conditions beyond those used to inform the models and the effects of clamping were minimal and did not influence our final results (see Appendix S2 in Supporting Information). Although we deem the ENM calibration decisions presented above (i.e. use of PCA-transformed instead of raw bioclim layers, the number and type of features used and the background extent used) to be best-practice for our specific objectives, we nonetheless conducted a sensitivity analysis to evaluate the effects of these decisions on our final conclusions (Appendix S3).

Predictions about the suitability of TE sites were based on ENMs generated from the full locality data set for each species and maxent's logistic output (with the default prevalence setting of 0.5; our tests relied on the relative suitability of sites within species and the use of logistic vs. raw output did not affect our final results). However, model evaluation was based on one of two methods. For species with at least 25 unique locality records ($N = 36$), we randomly split the locality data into five unique subsets and built five models, withholding one fold of the data to serve as an evaluation data set during each round of model calibration (i.e. five-fold 'cross-validation': Fielding & Bell 1997). For the four species with < 25 unique locality records, model evaluation followed the method of Raes & ter Steege (2007). Specifically, we compared the AUC score from the model to a null distribution of scores based on 99 models built using random points from within the species' range. Models were considered to outperform random models if the observed AUC was within the upper 97.5% tail of this null distribution. Average AUC from the k-fold models for each species ranged from 0.73 to 1 (median: 0.88) with all species evaluated in this way having at least one estimate of AUC ≥ 0.75. The ENM of the four species evaluated against a null distribution of AUC scores all passed model evaluation.

Testing for declines in fitness and suitability

We generated linear mixed-effects models using the *nlme* package in R (Pinheiro *et al.* 2013) to independently test for declines in individual fitness and the suitability of sites across range limits. In both cases, values of the response variable (best-proxy fitness or predicted suitability) were based on sites included in the transplant studies, with values standardised across sites according to the equation: (value at site i – mean value across all sites)/mean value across all sites. We note that it was not possible to weight fitness values at each site by their standard error or deviation as this information was only provided for 35% of the species. To better meet model assumptions, standardised fitness (initially ranging from -1 to 1) was log-transformed after adding a value of two to make all estimates positive. Site type (in-range vs. over-the-edge) was a fixed factor and species a random effect in all models (with species nested within study in the fitness models). The analysis was run with all range limits combined as well as for horizontal and vertical range limits separately. Although we might expect differences between other types of edges (i.e. poleward limits may be more likely to be dispersal limited following deglaciation than equatorward limits: Svenning *et al.* 2008), small sample sizes did not permit us to directly test these predictions. To explore the effects of combining fitness proxies, we also ran the analyses pertaining to fitness using subsets of species for which different fitness proxies had been reported (Appendix S3).

Covariates considered in the fitness models were fitness proxy, number of study sites, the life-history stage of transplanted individuals (seed/larvae, juvenile, adult) and study duration. Covariates considered in the suitability models were the median pairwise distance between in-range and over-the-edge sites, range size (estimated as the area of the MCP) and the number of localities used to build the ENMs (along with the interaction between the latter two). Covariates had correlation coefficients < 0.6 and thus were considered independent. We first ranked all possible model combinations based on AIC (or AIC_c for tests where $N < 40$) using the *MuMIn* package in R (Barton 2014). We then evaluated the fit of competing models (i.e. models with delta AIC < 2 relative to the model with the lowest AIC score) using likelihood ratio tests (full model compared to a reduced one) with the intention of using model averaging if more than one model had significant covariates. However, covariates were not significant in any of the competing models and were thus dropped from the final model for simplicity.

Testing concordance between transplant studies and niche models

We used a sign test to determine whether TEs and ENMs generally led to similar conclusions as to whether range limits are niche limits within species. For each species, we noted the direction of the difference between the median fitness of over-the-edge vs. in-range sites and the direction of difference between the median predicted suitability of over-the-edge vs. in-range sites. Transplant results were considered concordant with ENM predictions when these differences were both negative (consistent with niche limitation) or both non-negative (consistent with dispersal limitation; Fig. 1). Results were considered discordant if one approach led to a negative difference between in-range and over-the-edge sites and the other did not (Fig. 1). The *binom.test* function in R was used to run sign tests for horizontal and vertical range limits together and separately, with the expected frequency of agreement between approaches (e.g. 'successes') set to 0.5 in all cases.

RESULTS

Across species, both the fitness of transplanted individuals and the predicted suitability of sites was significantly lower outside the range than inside the range when all range limits were considered together (i.e. when sites were defined as being in-range or over-the-edge regardless of range edge type; Fig. 2a,b; Table 2). None of the covariates tested were significant. Conclusions about the causes of range limits were highly concordant across ENMs and TEs within species when all range types were considered together (Exact Binomial Test: 31 concordant out of 40 trials, $P = 0.00068$). Consistent with niche limitation, fitness and suitability declined across range limits for the 31 species demonstrating concordance. Of the nine cases where the results from the two methodologies were discordant, eight resulted from a decline in predicted suitability but not fitness across range limits, with only a single species demonstrating the opposite pattern (Table 1). No species demonstrated patterns fully consistent with dispersal limitation (i.e. with neither fitness nor suitability declining across range limits). These results were maintained when different fitness components were analysed separately (Table S3-1) and were largely robust to different decisions made during ENM calibration (Tables S3-2 to S3-6).

Both fitness and suitability also declined from in-range to over-the-edge sites when horizontal and vertical range limits were treated separately (Fig. 2c–f; Tables 2, S3-2). When partitioned by range type, conclusions from TE and ENMs within species were also often concordant, however, the frequency of concordance was only statistically different from 0.5 for vertical range limits (vertical: 15 concordant out of 19 trials, $P = 0.019$; horizontal: 17 out of 25, $P = 0.11$) and in this case, did show sensitivity to some of the decisions made during ENM calibration (Table S3-3).

DISCUSSION

Our study sheds new light on the extent to which generalisations about the causes of species' geographical range limits

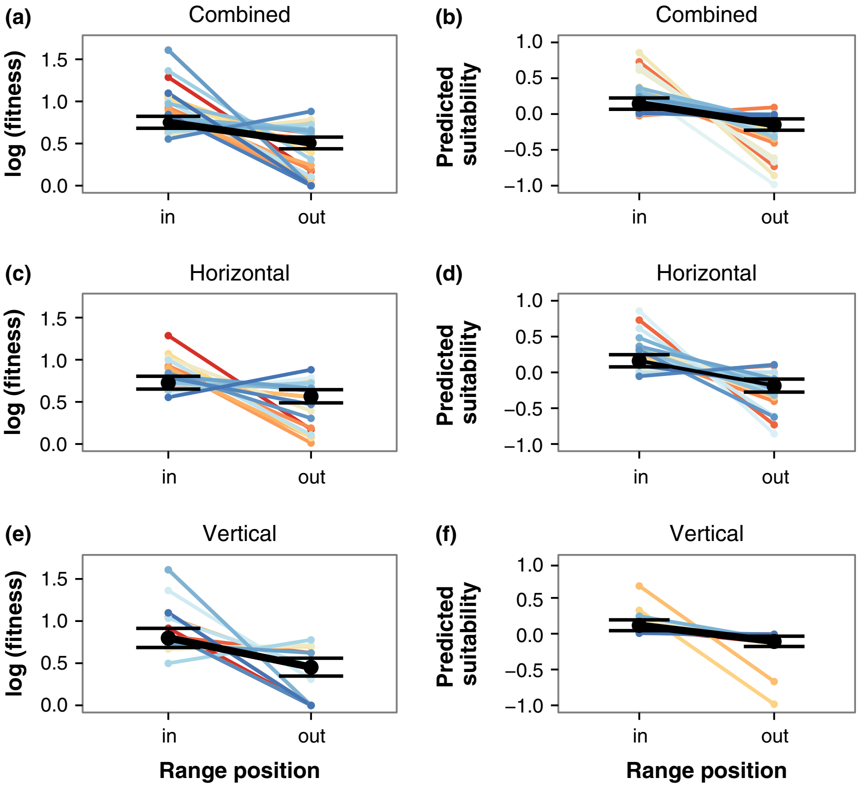


Fig. 2 Differences in the mean fitness of transplants (left panels) and the mean suitability of sites (right panels) across range limits for all range limits combined (a, b), and for horizontal (c, d) and vertical (e, f) range limits separately. Coloured lines in both panels represent different species. Overall model means and 95% confidence intervals for in-range and over-the-edge sites are shown in black.

Table 2 Differences in the fitness of transplanted individuals and suitability of sites across different types of range limits (with 95% confidence intervals around the mean coefficient). Negative coefficients indicate that fitness or suitability was lower for over-the-edge sites compared to in-range sites. Comparisons between the full and reduced model (i.e. without site type) were based on likelihood ratio tests (LRT). Significant values ($P < 0.05$) are in bold

Response	Type of limit	Mean coefficient (SE)	95% confidence interval	LRT	*P* value
Fitness	Combined*	−0.25 (0.049)	−0.40, −0.28	$\text{LRT}_{7,6} = 21.03$	**< 0.0001**
	Horizontal*	−0.16 (0.055)	−0.22, −0.11	$\text{LRT}_{6,5} = 8.38$	**0.0038**
	Vertical*	−0.35 (0.077)	−0.42, −0.27	$\text{LRT}_{7,6} = 13.58$	**< 0.0001**
Suitability	Combined	−0.29 (0.056)	−0.35, −0.24	$\text{LRT}_{4,3} = 25.50$	**< 0.0001**
	Horizontal	−0.35 (0.063)	−0.41, −0.28	$\text{LRT}_{4,3} = 27.24$	**< 0.0001**
	Vertical	−0.22 (0.053)	−0.28, −0.17	$\text{LRT}_{4,3} = 16.70$	**< 0.0001**

*To improve homoscedasticity, variances were allowed to vary by a fixed or random effect if the model fit was significantly improved. In this case, variances were allowed to vary by the type of fitness estimate.

can be made (e.g. Gaston 2009). Across species results from TEs and ENMs independently supported the hypothesis that range limits reflect niche limits. Importantly, inferences from the two approaches were generally concordant within species, with most species appearing to be niche limited (although there were differences in the extent of concordance when horizontal and vertical range limits were analysed separately). This intersection of results, across multiple species and methods, provides compelling support for the hypothesis that range limits are often niche limits. We discuss the implications of these findings for our understanding of species' range limits.

Range limits are often niche limits

Across species, results from both TEs and ENMs were more consistent with niche constraints on range limits than with dispersal limitation. Hargreaves *et al.* (2014) previously surveyed the TE literature and reported frequent declines in fitness across range limits. Our independent survey of the literature confirms this result, despite some differences in the species considered and analytical framework used. As a separate and novel line of investigation into the role of niche constraints on range limits, we asked whether the predicted suitability of sites declined across range limits and found this to be the case for 97.5% of the species represented by the TEs. Joint consideration of the results from both lines of investigation within species also supported the hypothesis that range limits reflect niche limits, with 31 out of the 40 the species surveyed demonstrating declines in both fitness and suitability across range limits and no species demonstrating patterns of fitness and suitability fully consistent with dispersal limitation.

Differences between vertical vs. horizontal range limits

Fitness and suitability declined across range limits and the results from TEs and ENMs remained mainly concordant when horizontal and vertical range limits were examined separately. However, the frequency of agreement between TEs and ENMs was only statistically significant for vertical range limits. The smaller sample sizes that resulted from splitting the data by range type may have reduced the statistical power of our tests. Alternatively, this result may reflect real differences in the importance of niche limitation for horizontal vs. vertical range limits. Steeper environmental gradients with changes in elevation (as opposed to latitude or longitude) may mean that niche limitation is more important to vertical than to horizontal range limits, with dispersal limitation playing a greater role for some horizontal range limits (Hargreaves *et al.* 2014) and perhaps being harder to detect with the ENMs (for six out of the eight cases of discordance for horizontal range limits suitability declined but fitness did not). However, a number of issues can affect the conclusions drawn from TEs and ENMs and so it is difficult to attribute particular cases of discordance to the failure of one type of analysis or the other (see Fig. 1; discussed below). Given the limited sample sizes available for testing the causes of horizontal and vertical range limits separately, and that the majority of horizontal and vertical cases mirrored the general pattern observed in the larger analysis of all range limits combined (i.e. with most species demonstrating patterns fully consistent with niche limitation), we focus on the signal of niche limitation observed in our analyses.

Which niche?

A full review of niche concepts is beyond the scope of this paper (see Chase & Leibold 2003 and Soberón 2007 for reviews). However, if inferences from TEs and ENMs are to be informative for understanding the specific processes that govern species' distributions, some discussion of what these studies measure is pertinent. As commonly implemented, both types of study better address the niche as habitat (i.e. Grinnell 1917; Hutchinson 1957) than the niche as function (i.e. Elton 1927). Furthermore, at least in the short term, both methods better speak to what Hutchinson (1978) referred to as *scenopoetic* or frequency-independent variables (as opposed to *bionomic* variables or resources that can be consumed and are influenced by the species themselves: see Soberón (2007) for review). Thus, our results suggest that species are often limited by the availability of immediately suitable habitat, defined by environmental variables that are relatively unaffected by the species themselves.

The frequent concordant declines in both fitness and suitability suggest that the specific factors driving range limits are those that transcend the scales of both types of study. Our use of climatic variables in the ENMs would suggest that range-limiting factors are often climate-related. However, the climatic tolerances of species may not directly impose range limits. Any biotic factor (or abiotic factor not included in the model) that influences presence on the landscape will influence ENM predictions through effects on the calibration data. For this reason, correlative ENMs are generally expected to model something closer to the realised rather than the fundamental niche of a species (Sillero 2011; Wisz *et al.* 2013). However, only those biotic interactions that systemically exclude a species from regions of climatic space that it could otherwise occupy are expected to influence ENMs based on climatic variables (Peterson *et al.* 2011). More localised biotic interactions captured by the TEs are unlikely to be represented by coarse-scale ENMs (e.g. Soberón 2007; Peterson *et al.* 2011). Thus, our results suggest that where biotic interactions exert an effect on range limits, they do so at spatial scales commensurate with broad-scale climatic variables. Likewise, as these effects would have to be associated with climate to influence model predictions, our results indicate that the role of climate on range limits, though possibly indirect, is important.

Designing better individual studies

Although inferences from TEs and ENMs were largely concordant, cases of discordance highlight the potential for issues with the design of either TEs or ENMs to limit the conclusions that can be drawn for any given species. We next discuss measures that can be taken to avoid such issues when designing individual studies.

Transplant experiments

Lack of information about lifetime fitness is an important limitation of many TEs (see also Hargreaves *et al.* 2014). Differences in performance across range limits as measured by individual fitness components may fail to represent overall differences in fitness if success at one life stage is countered by failure at another, or *vice versa*. However, regardless of whether a given fitness proxy accurately captures relative differences in overall fitness, the question of whether range limits are niche limits ultimately requires evaluation of whether populations can persist beyond the range. Only those studies that evaluate lifetime fitness or population growth rates at over-the-edge sites can fully address this question. Of the 40 species surveyed here, lifetime fitness was only reported for six (all moved over a horizontal limit). In four cases (noted in Table 1), conclusions about niche limitation based on relative differences in fitness were consistent with conclusions that would be made based on the potential for persistence. However, for two species, conclusions based on relative fitness differences across the range were not well-matched by patterns of absolute fitness. Both of these species showed declines in relative fitness across range limits, but one had positive (*Camissoniopsis cheiranthifolia*) and the other had negative population growth rates (*Chamaecrista fasciculate*) both inside and outside the range. Thus, relative differences in fitness do not always indicate differences in the ability to maintain populations beyond the range.

Proper replication across space is also necessary to ensure that the results from TEs are not driven by site effects. Without replication, the unintentional use of sinks as in-range controls may mean that individuals do just as well (i.e. poorly) when moved across range limits, despite a range limit that is truly a niche limit. Likewise, even when range limits fall short of niche limits, not all locations beyond the range will meet the requirements of a given species and individuals inadvertently transplanted to low-quality sites beyond the range may mislead transplant studies in the opposite direction. Including multiple in-range controls and over-the-edge sites reduces the influence of these types of site effects on the overall results from transplant studies, yet most of the studies surveyed were not properly replicated in this way (Tables 1 and S1-1).

Replication over time is also important. In particular, results from a short-term TE may be a poor indication of a species' ability to succeed or persist beyond the range if atypical conditions occur during the study period. A particularly favourable year may afford individuals unusually high success beyond the range, causing investigators to miss real constraints on establishment. Likewise, a period of unusually bad conditions may cause transplanted individuals to fail where they would usually succeed, misleading conclusions in the opposite direction. Only six TEs were fully replicated across time. Furthermore, only seven studies explicitly discussed the extent to which conditions during the study period were representative of average conditions. Thus, the influence of year effects on conclusions from over-the-edge transplant studies is under-assessed to date. This oversight is unfortunate given that extreme climate years beyond the range may, in and of themselves, be an explanation for range limits (e.g. Gray *et al.* 2006; Jackson *et al.* 2009).

Niche models

A number of methodological challenges concerning ENMs have been discussed in the literature. These include issues surrounding precision, sampling bias and autocorrelation in the locality data set (Graham *et al.* 2007; Veloz 2009; Hijmans 2012; Varela *et al.* 2014); limitations of available environmental data sets (both in terms of resolution and quality, as well as variables represented: Guisan *et al.* 2007; Thibaud *et al.* 2014); and the impact of algorithm choice (Araújo & New 2007; Elith & Graham 2009; Thibaud *et al.* 2014) and parameterisation (Warren & Seifert 2011; Merow *et al.* 2013) on model predictions. Although we attempted to address several of the bigger challenges in our analysis, best practices will vary by species and specific study objectives. Individual studies using ENMs to study range limits should address these issues explicitly, fully document the decision-making process when there are alternative ways of doing things, and conduct sensitivity analyses to evaluate the impact of decisions made during calibration on final conclusions. Based on our own sensitivity analyses, we note that conclusions about the extent to which suitability declines across range limits were sensitive to some of our modelling decisions for some species in particular (Tables S3-4, 5, 6). However, the majority of models for the species in question were consistent in their conclusions and there was no indication that any single modelling decision systematically changed the conclusions for a large number of species. Furthermore, our overall conclusions were largely insensitive to how the ENMs were calibrated (Tables S3-2, S3-3). Only the significance of the test of the frequency of concordance between TEs and ENMs for vertical limits varied across the different niche modelling iterations, with this outcome being largely driven by changes in model predictions for two or three species.

Regardless of the possible effects of decisions made during model calibration, we note that even the most carefully calibrated ENM cannot overcome the limitations of relying on occurrence data to infer the effects of environmental conditions on individuals and populations (e.g. see Fig. 7 in Araújo *et al.* 2013). In this regard, mechanistic niche models, based on direct experimentation (e.g. Kearney & Porter 2009), are expected to better address fundamental niche limits and their use should be encouraged. However, recognising that direct experimentation is often not possible, we recommend that investigators exercise caution when deciding on a locality data set for correlative ENMs. For practical reasons, our ENMs relied on GBIF data. We took several measures to assess the quality of and filter these records and do not expect noise in these data to bias our overall conclusions. However, many sources of locality information, including GBIF, are compilations of data that were not explicitly collected for niche modelling purposes. Care is needed when relying on data from these types of sources (Lozier *et al.* 2009) and where possible, investigators should strive to conduct their own locality surveys, following best practices for niche modelling (e.g. avoiding sampling bias, sampling at scales appropriate for the questions at hand and for the resolution of the environmental data set, ensuring independence of training and testing data sets, etc.) and collecting true absence data.

The value of a combined approach

Our analysis adds to a growing number of studies that have examined niche model predictions (or related estimates of niche centrality) with respect to other types of information about populations (e.g. genetic diversity: Lira-Noriega & Manthey 2014; population density: Tôrres *et al.* 2012; abundance: Martínez-Meyer *et al.* 2013). In the case of TEs and ENMs, we propose that, in addition to the benefits of basing conclusions about range limits on multiple lines of investigation, the two approaches can be used iteratively towards a more robust framework for studying range limits (Fig. 3). For example ENMs may help identify occupied sites of relatively low suitability that should be excluded as in-range controls when choosing TE sites and may also inform predictions about relative performance at different locations beyond the range. ENMs may also help identify the effects of climatically unusual years on transplant success in cases where these effects cannot be directly accounted for in experimental design. Specifically, model predictions based on conditions during the year of study for a given site could be compared to a distribution of year-specific predictions across a relevant time period, or to predictions based on long-term average conditions, to identify potential climatic anomalies that may have caused transplant sites to be unusually suitable or unsuitable during the study period.

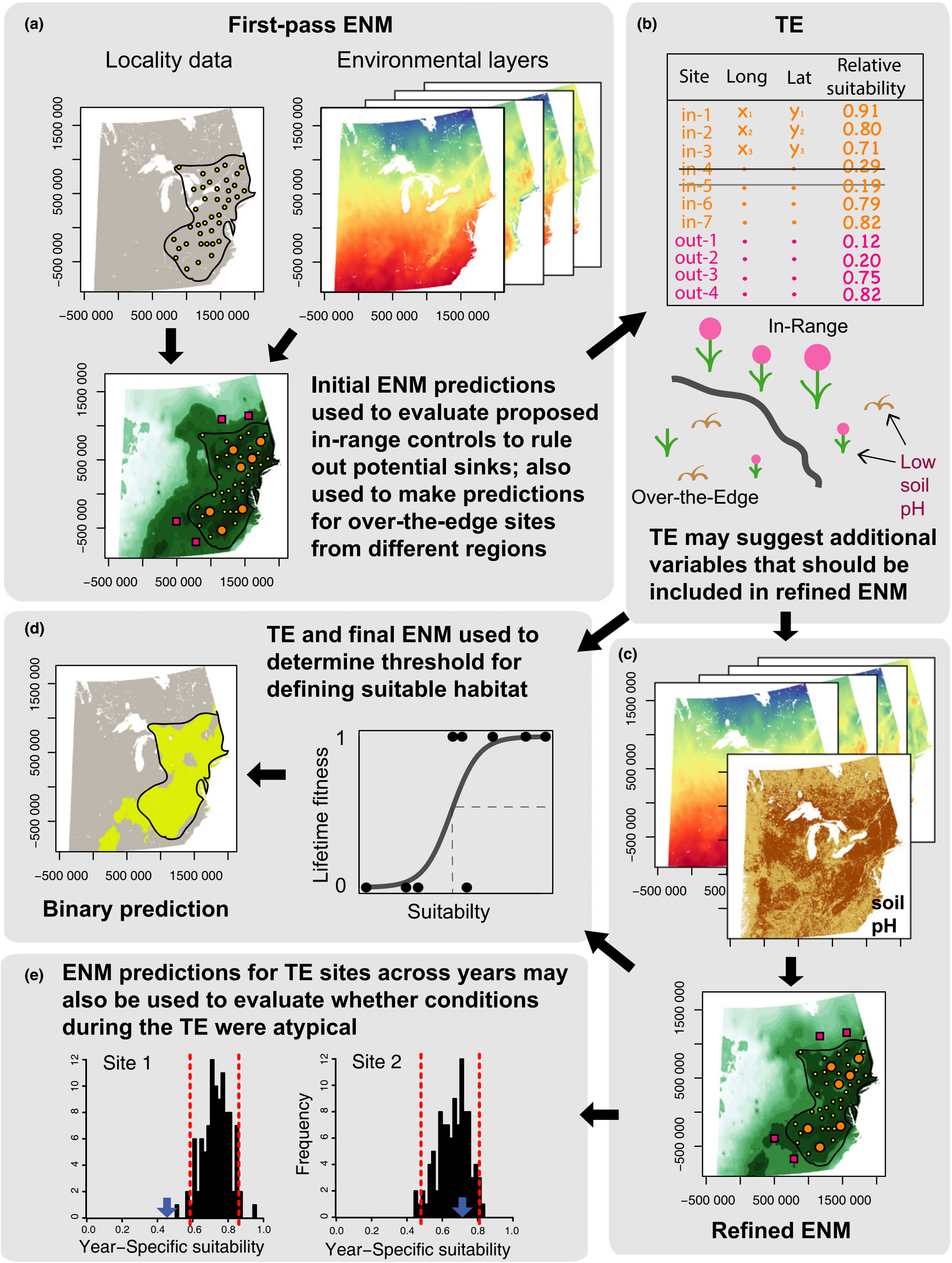


Fig. 3 An integrative framework for testing whether range limits are niche limits using niche models (ENMs) and transplant experiments (TEs). In our hypothetical example, an initial ENM (a) is used to make predictions about the relative suitability of proposed transplant sites (orange circles and pink squares in the maps with green shading). The TE is conducted after excluding in-range controls of relatively low suitability (i.e. potential sinks) (b). The TE may motivate another round of niche modelling to incorporate additional variables that influence transplant success (c). An appropriate threshold for converting continuous ENM predictions into binary habitat maps is determined from the relationship between absolute fitness and predicted suitability (d). ENM predictions for each site based on the conditions experienced during the study year can be compared to the distribution of predictions for other years (e) to assess whether the TE year was atypical (‘Site 1’ in our example).

In turn, observations made during TEs (e.g. effects of herbivores on survival, more limited success on some substrates than others, etc.) may point to additional variables that can be used to refine ENMs. TEs that measure lifetime fitness across multiple sites can also inform appropriate thresholds of suitability when converting continuous niche model predictions into binary maps of suitable vs. unsuitable habitat. For instance using the inflection point from a logistic regression of suitability vs. transplant success (i.e. where success is defined as lifetime fitness ≥ 1) as the cut-off for considering a site as suitable or not would lead to more biologically informed suitability maps than existing thresholds (see Table 7-1 in Peterson *et al*. 2011 for review of commonly used thresholds; see also Eckhart *et al*. 2011 for an alternative way to use fitness data at the ENM calibration stage). It follows that a combined approach would lead to better quantification of both the relative proportion of suitable to unsuitable habitat beyond the range, as well as the proximity (relative to the dispersal capabilities of a focal species) of any suitable habitat to the range edge.

Final remarks

Our results suggest that range limits are commonly niche limits and thus raise questions about the relative importance of dispersal limitation to species' distributions. This result is particularly striking given the preponderance of sessile taxa in our data set (most of the studies included here were plants). However, additional work is needed to distinguish the relative importance of niche limitation vs. dispersal limitation for a greater number of taxonomic groups and for different types of range limits, including the horizontal and vertical range limits examined here. Apart from possible differences between horizontal and vertical range limits, we note that not very many of the TEs surveyed addressed range limits in the context of contact zones between closely related species (only the *Clarkia* and *Mimulus* experiments could be used for this purpose). Such parapatric range limits may account for a large proportion of range limits (e.g. Hewitt 1989). Dispersal barriers may play an important role shaping the location of these types of limits (Glor & Warren 2011), especially where taxa hybridise (Goldberg & Lande 2007). Furthermore, dispersal limitation is likely to become more prevalent as human-driven reductions in landscape connectivity prevent species from tracking shifts in the distribution of suitable habitat under ongoing climate change (Lawler *et al*. 2013). Thus, the potential importance of dispersal limitation in shaping present and future patterns of biodiversity should not be discounted. At the same time, our results underscore the importance of limits to adaptation in shaping contemporary distributions (Bridle & Vines 2007). Moving forward, studies aimed at identifying the specific traits and genes imposing these limits will afford us a better understanding of the specific processes governing species' range limits.

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AUTHOR CONTRIBUTIONS

All authors contributed substantially to this study. The initial idea for the study was conceived of during a conversation between JAL and ALA and developed further by all authors. Data from the transplant literature were assembled by MB, ALA, AN and CM. Data for the niche models were collected and processed by AMC, QL, HMK and RS. JAL built the niche models with help from RS. HMK conducted the statistical analyses with input from JAL, RS, CM and ALA. JAL wrote the manuscript in consultation with all authors, and with particularly critical input from HMK, CM, MB and ALA.

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SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library: (www.ecologyletters.com). Data and R scripts are available on figshare at: https://dx.doi.org/10.6084/m9.figshare.3123931.v1

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