A meta-analysis of plant facilitation in coastal dune systems: responses, regions, and research gaps

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Empirical studies in salt marshes, arid, and alpine systems support the hypothesis that facilitation between plants is an important ecological process in severe or 'stressful' environments. Coastal dunes are both abiotically stressful and frequently disturbed systems. Facilitation has been documented, but the evidence to date has not been synthesized. We did a systematic review with meta-analysis to highlight general research gaps in the study of plant interactions in coastal dunes and examine if regional and local factors influence the magnitude of facilitation in these systems. The 32 studies included in the systematic review were done in coastal dunes located in 13 countries around the world but the majority was in the temperate zone (63%). Most of the studies adopt only an observational approach to make inferences about facilitative interactions whereas only 28% of the studies used both observational and experimental approaches. Among the factors we tested, only geographic region mediates the occurrence of facilitation more broadly in coastal dune systems. The presence of a neighbor positively influenced growth and survival in the tropics whereas in temperate and subartic regions the effect was neutral for both response variables. We found no evidence that climatic and local factors, such as life-form and life stage of interacting plants affect the magnitude of facilitation in coastal dunes. Overall, conclusions about plant facilitation in coastal dunes depend on the response variable measured, and more broadly, on the geographic region examined. However, the high variability and the limited number of studies, especially in tropical region, indicate we need to be cautious in the generalization of the conclusions. Anyway, coastal dunes provide an important means to explore topical issues in facilitation research including context dependency, local versus regional drivers of community structure, and the importance of gradients in shaping the outcome of net interactions.

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13 **Introduction**

14 The role of positive interactions, or facilitation, between plants as key drivers of plant community

15 dynamics and structure is widely recognized and reviewed (Brooker et al., 2008; McIntire & Fajardo

16 2014). Most empirical studies show that facilitative effects are more important in severe environments

17 because neighbors frequently buffer other individuals from abiotic stressors (He, Bertness & Altieri,

18 2013). The classical systems that generated this research topic are deserts (Franco & Nobel, 1989;

19 Flores & Jurado, 2003), salt marshes (Bertness & Hacker, 1994; Bertness & Leonard, 1997), and more

20 recently, alpine systems (Badano et al., 2006; Cavieres et al., 2014). However, positive interactions

21 may also be important in many other ecosystems, and there are similar gradients that likely shift the

22 relative frequency of positive interactions.

23 Recent research in coastal dune vegetation has increasingly focused on facilitation between

24 plants. Coastal dune vegetation, here defined as a mosaic of plant communities in the coast that occupy

25 sandy plains formed by marine deposits (modified from Scarano 2002), is both stressful and highly

26 disturbed, with soil moisture and nutrient limitations, wind exposure, sand burial, salt spray and soil

27 salinity, potentially negatively impacting plants (Wilson & Sykes, 1999). Similar to desert systems, the

28 presence of some plants, such as shrubs, ameliorate some of these limiting factors and can provide an

29 opportunity for association by other species (Martínez & García-Franco 2004). Several studies in

30 coastal dunes have shown that the performance of plants established in the neighborhood of other

31 plants are higher than in open areas (Shumway, 2000; Martínez, 2003; Forey et al., 2009; Castanho &

32 Prado, 2014). However, the occurrence and intensity of facilitation in coastal dunes is also highly

33 variable within and between the studies (Forey et al., 2009; Castanho, Oliveira & Prado, 2012) thereby

34 suggesting that facilitation is dependent on the local environmental conditions or the gradients (He,

35 Bertness & Altieri, 2013) and also on the traits of interacting plants (Soliveres et al., 2014). As

36 demonstrated in dunes and other systems, the magnitude of facilitation depends on plant life-stage

37   (Miriti, 2006; Armas & Pugnaire, 2009) and plant life-form (Gómez-Aparicio, 2009; Castanho,

38   Oliveira & Prado, 2012) with higher intensities associated with adult woody benefactors and woody

39   beneficiary species at relatively earlier life-stages. Furthermore, the enviromental severity also shapes

40   the outcome of interactions with more intense facilitation commonly detected under increasingly harsh

41   conditions (He, Bertness & Altieri, 2013). Consequently, coastal dunes may also be an ideal system to

42   explore net interactions in plants communities, but without synthesis, the context dependency of these

43   positive interactions is not broadly accessible (Gómez-Aparicio, 2009) and research gaps are not easily

44   identified.

45   Hence, a formal quantitative analysis of the literature in these systems is required. Such analysis

46   can provide an estimate of the general influence of facilitation on the organization and dynamics of the

47   coastal dunes, further the scope of hypothesis testing in this ecological subdiscipline, and contrast the

48   relative importance of local versus regional drivers of plant community structure (Thebault et al.,

49   2014). We note that the scale of drivers of community structure is an important contemporary issue in

50   ecology (Powers et al., 2009; O'Halloran et al., 2013) that most likely needs to be resolved on an

51   ecosystem-by-ecosystem basis. Moreover, the restoration of degraded coastal dunes is a pressing issue

52   in many regions of the world (Lithgow et al., 2013), and facilitation by dominant coastal plant species

53   is an obvious potential management solution.

54   To meet these research needs, we present a systematic review and meta-analysis of facilitation

55   in coastal dune plant communities. The systematic review synthesizes current literature and highlights

56   research gaps, while the meta-analysis tests if factors at distinct scales (local versus regional) such as

57   environmental severity, life-form, or life-stage of the interacting plants significantly explained the

58   variation in the intensity of plant facilitation in coastal dunes.

59

60   **Materials & Methods**

61 *Data collection*

62 We conducted a survey of the published studies that explicitly tested for the presence of facilitation

63 between plants in coastal dunes. The literature was queried by using ISI Web of Science in June 2013

64 by using a combination of three groups of terms: i) "dune*" or "restinga" or "coastal sand vegetation",

65 and ii) "facilitation" or "positive interaction*" and iii) "plant*" or "tree*" or "shrub*" or "herb*". We

66 did not include competition studies because our main aim was to test factors that affect the intensity of

67 facilitation in dunes and not to make inferences about the importance of facilitation relative to

68 competition. The search led to 90 publications that were subsequently examined firstly for their

69 suitability in the review and secondly in the meta-analysis. For the first selection criterion, only studies

70 that explicitly examined facilitation between plants in coastal dune vegetation under field conditions

71 were included (n=32). Reviews, studies on non-coastal dunes, and those in which at least one of the

72 interacting organisms were not a plant were excluded. To conduct the meta-analysis, the studies also

73 had to include the following: i) data reported in a usable form; and ii) the effect of neighbors on target

74 species compared to the performance of plants without neighbors. When the required data were only

75 reported in graphical form, the graphics were scanned and extracted in table format using TechDig

76 software (Jones, 1998). Multiple outcomes per publication that tested different combinations of

77 neighbor-target species, different life stages, or different sites were treated as independent outcomes.

78 However, if repeated measures were taken from the same experiment, only the results reported at the

79 completion of the experiment were used. Similarly, only the final year in multi-year experiments was

80 used as a conservative estimate of impacts and to avoid pseudoreplication issues. Furthermore, if

81 additional treatment such as water or fertility addition was performed, we only used the estimates from

82 the control level (no addition) because it better approximates the natural/ambient conditions. Authors

83 of publications with unreported datasets were also contacted to secure data.

84   To understand how facilitation intensity varies among study outcomes, each outcome was

85   classified according to the following explanatory variables: neighbour and target life-forms, target life

86   stage, geographic regions and environmental severity. Regarding life-forms, neighbour and target

87   plants from each outcome was classified as tree, shrubs or herbs (which was further subdivided into

88   grass and forb when the information was available). For target life stage we classified the target plants

89   as seed, young (including seedlings, saplings and juveniles) or adult. We also classified each outcome

90   according to the geographic region, *i.e.*, as tropical (from latitude 0° to 28°), temperate (29° to 54°) and

91   subarctic-subantarctic (more than 55°) using the reported latitudes. Because of the coarse sand texture

92   of the soils, water is often a limiting resource in coastal dunes (Maun, 1994; Le Bagousse-Pinguet et

93   al., 2013). Therefore, we used mean annual precipitation (MAP) of each site as a proxy for

94   environmental severity. Based on the GPS coordinates listed in each paper, we extracted an estimate of

95   MAP for each study site from the meteorological forcing fields of the Global Land Data Assimilation

96   System, version 1 (GLDASv1). GLDAS is a global, high-resolution terrestrial modelling system that

97   incorporates satellite and ground-based observations in order to produce optimal fields of land surface

98   states and fluxes in near–real time (Rodell et al., 2004).

99   While MAP is one indicator of environmental severity, plant life at coastal dunes around the

100   world can be limited by a combination of factors such as nutrient limitation, salinity, and sand burial

101   (Maunn, 1994; Wilson & Sykes, 1999). The complex nature of coastal limiting factors typically

102   justifies the use of integrative proxies for environmental severity such as plant biomass (Dullinger et

103   al., 2007; Maestre et al. 2009). For this reason, we also used the normalized difference vegetation index

104   (NDVI), a proxy for plant biomass (Paruelo et al., 1997; Doiron et al., 2013), as an integrative variable

105   of environmental severity at both local and regional scales. To estimate the NDVI of each site, we used

106   remote sensing techniques and two kinds of images with different resolutions: Advanced Spaceborn

107   Thermal Emission and Reflection Radiometer (ASTER) images with 15 m resolution which provided a

108   local estimate of biomass vegetation; and Moderate Imaging Spectroradiometer (MODIS) images with

109   250m resolution which also provided a regional estimation. For the NDVI based on ASTER images

110   (hereafter called local NDVI), we used the coordinates and description of the site (Reserve, National

111   Park, etc) and local vegetation provided by each study in order to place the study site within the image

112   as precisely as possible. Then, the archive of ASTER images available for each site were searched and

113   images were selected at the same time as the study implementation and also to minimize cloud cover.

114   For the NDVI based on MODIS images (hereafter called regional NDVI), mensal images were used

115   from 2001 to 2009. In order to synthesize this information for each site, the mensal NDVI was summed

116   annually to calculate the mean annual NDVI. All NDVI calculation was done using the software

117   ERDAS IMAGINE 2011 (Intergraph; Madison, AL, USA).

118

119   *Meta Analysis*

120   Suitable studies were grouped into eight different datasets according to the plant response variable

121   reported: density, survival, growth (which includes biomass and growth in height), richness (number of

122   species), reproductive output (which includes any quantitative measure of flower, fruit or seeds

123   production), occurrence, and emergence. Because we had two types of response variables, we used

124   different measures of effect size: the natural log of the response ratio (ln (RR)) for continuous response

125   variables (density, growth, richness and reproductive output), and the natural log odds ratio (ln (OR))

126   for binomial response variables (survival, occurrence and seed emergence) (Rosenberg, Rothstein &

127   Gurevitch, 2013).

128   The natural log of the response ratio (ln (RR)) estimation, and its associated variance, was

129   calculated for each outcome using the mean, standard deviation (SD) and sample size (n) for control

130   (without neighbor) and treatment (with neighbor) (Rosenberg, Rothstein & Gurevitch, 2013). Values of

131 ln (RR) higher than 0 indicate a positive effect of the neighbor on the target performance (facilitation)

132 whilst values lower than 0 indicate a negative effect of the neighbor (competition). For categorical

133 responses, the natural log of the odds ratio (ln (OR)) and its associated variance for each outcome is

134 calculated using the number of success and failure occurrences for each treatment (Rosenberg,

135 Rothstein & Gurevitch, 2013). In the case of survival for example, this measure denotes the number of

136 survival and dead plants with and without neighbors, positive values of ln (OR) also indicate

137 facilitation. In the few cases where survival data were reported as mean and SD, we first calculated

138 Hedges g, converted to Cohen d, and finally to the common index ln (OR) in order to combine all

139 survival outcomes in the same meta-analysis (Borenstein et al., 2009).

140   The effect of the neighbor was assessed for each one of the response variable datasets that

141 included in at least five independent studies (this was a conservative threshold to ensure general value

142 to the synthesis). We used a threshold to avoid potential biases from trends associated too few studies.

143 Bias-corrected bootstrap 95% confidence intervals (CIs) were calculated for each overall effect size. If

144 the CI did not overlap zero, the effect was considered significant (Rosenberg, 2013). The Q-statistics

145 were used for each dataset in order to examine the heterogeneity among the effect sizes, and the

146 proportion of true variance in the effect sizes explained by each independent variable was estimated as

147 R^2 (Borenstein et al., 2009). The significance of the model structure was tested by randomization tests

148 with 9999 iterations (α= 0.05). The independent variables selected were i) geographic region (tropical,

149 temperate and subarctic-subantarctic regions), ii) neighbor life-form (i.e. tree, shrub, grass or forb); iii)

150 target life-form (i.e. tree, shrub, grass or forb); iv) target life stage; v) mean annual precipitation

151 (MAP); vi) local NDVI; and vii) regional NDVI.

152   Data were analyzed using mixed-effect models, that encompass both fixed and random effects,

153 with fixed differences among predictors (continuous or categorical covariates) and random variation

154 among studies within levels of the predictor, as well sampling error within studies (Mergersen et al.,

155 2013). In the present context, the random variation among studies are more reasonable than fixed

156 variation because the complex interactions in ecology generally result in ecologically important

157 heterogeneity between studies (Pullin & Stewart, 2006). Additionally, the use of mixed-effect models

158 (with random variation among studies instead of fixed variation) fits the goal of generalization usually

159 present in similar reviews (Borenstein et al., 2009). We tested publication bias calculating the

160 Rosenthal's fail number, specifically, that a fail-safe number larger than $5n + 10$ (where n is the

161 number of outcomes) is a conservative critical value (Rosenthal, 1979). Funnel plots with Kendall's tau

162 rank correlation tests were also examined to explore potential publication bias. We used the R

163 environment (version 3.1, R Core Team 2014) with the package metafor (Viechtbauer, 2010) for all

164 statistical analysis.

165

166 **Results**

167 *Systematic Review*

168 From 90 articles identified through database searching, a total of 32 articles met the selection criteria

169 for the systematic review (Supplemental Table S1). A PRISMA flow diagram was generated (Moher et

170 al., 2009) outlining the publication selection process (Fig. 1). These articles were published in 16

171 different journals between 1997 and 2013. These studies were performed in 13 countries, but a total of

172 31% of all studies were done on coastal dunes in the USA. With respect to diversity of climatic zones

173 examined, 63% of the studies were done in the temperate zone, 28% in the tropics, and 9% in the

174 arctic-subarctic zone. A total of 15 studies, i.e. 47%, were observational and 8 (25%) were

175 manipulative whilst 9 studies (28%) used both approaches. A total of 362 independent outcomes were

176 extracted for the seven plant performance response variables. Density was the most frequent

177 representing 31% of the total, followed by survival (22%), growth (18%), reproductive output (12%),

178 richness (8%), occurrence (7%) and emergence (2%). The earlier life stages for target plant species

179 were most represented in these studies (i.e., seedlings, saplings, and juveniles) with 43% of the total

180 number of measurements versus 20% of studies recording adults. Shrubs were the most common nurse-

181 plants examined representing 46% of the outcomes, followed by herb (36%), tree (9%), moss and

182 lichen (4%) and a mix of life-forms used in 4% of the outcomes. The most common target life-forms

183 were herb (51%), followed by mix of life-forms (24%), shrub (19%), tree (4%), liana (1%) and moss

184 (1%).

185

186 *Meta-analysis*

187 A total of 160 independent effect size estimates were suitable for the meta-analysis component

188 of this synthesis (Table 1). Density (Supplemental Table S2), growth (Supplemental Table S3) and

189 survival (Supplemental Table S4) datasets provided sufficient independent studies, i.e. at least 5 studies

190 and 10 effect sizes (outcomes), to be considered in the meta-analysis (Table 1). There was no evidence

191 of publication bias for density and growth (Kendall's tau= 0.14, P= 0.22 for density; Kendall's tau=

192 0.06, P= 0.58 for growth) and a limited indication of bias for survival (Kendall's tau= -0.23, P= 0.04).

193 The fail-safe numbers indicated that the results detected for density and survival could be driven by

194 limited or biased sets of publications available for synthesis (for density: critical threshold= 210, fail-

195 safe number= 181; for growth: critical threshold= 205, fail-safe number= 468, for survival: critical

196 threshold= 220, fail-safe number= 40).

197 Across all study outcomes, the presence of neighbor had no effect on the density of the target

198 species examined (mean lnRR = 0.38, 95% confidence intervals: -0.13-0.88). However, the overall

199 heterogeneity test was significant indicating that the different study outcomes do not share a common

200 effect and explanatory variables may explain the observed variability among study outcomes (Q=644;

201 df= 39, P< 0.0001). However, the variability in effect sizes for plant density were not explained by any

202   of the factors we considered (Table 2). The presence of neighbors had a positive effect on the growth

203   of the target species (Fig. 2A). The overall heterogeneity test was significant (Q=186; df= 38, P<

204   0.0001) but only geographic region factor was a significant predictor of the variability amongst

205   outcomes (Table 2). In the temperate and subarctic regions, there is no evidence of neighboring effect

206   on target growth (Fig. 2A). In the tropics, the presence of neighbor increased the growth of target

207   species (Fig. 2A). The survival of target plants was not significant affected by the presence of

208   neighbors (Fig. 2B). The test of within-study heterogeneity was significant (Q=178; df= 41, P< 0.001),

209   but again only geographic region was a significant explanatory factor (Table 2). Target plant survival

210   in tropical regions was increased by neighbours but not in the coastal dunes from temperate regions

211   (Fig. 2B).

212

213   **Discussion**

214   Empirical studies support the hypothesis that facilitation between plants is an important ecological

215   process in severe environments (Brooker et al., 2008) including as demonstrated herein coastal dunes.

216   The first goal of the systematic review was to highlight general research gaps in the plant facilitation

217   research in coastal dunes. We found a clear concentration of dune facilitation studies in temperate

218   dunes indicating that to assess the impact of climate differences and gradients on facilitation between

219   plants future studies need to be done in other dune systems such as the tropics. The systematic review

220   also identified a predominance of observational studies over experimental studies, and this is

221   unfortunate in many respects given that the former is a weaker form of inductive inference. The second

222   goal of this study was to examine the importance of factors quantitatively and contrast different scales

223   of drivers on interaction strengths. The response variables measured in facilitation studies were an

224   important determinant of the factors determining the strength of interactions. For the three response

225   variables considered (density, growth, and survival), we found significant evidence for the importance

226   of geographic region in determining the magnitude of facilitation, but no evidence for the effects of

227   climatic and local factors within a region such as life form and life stage of the interacting species.

228   Collectively, this indicates that facilitation is important in coastal dunes and that its relative intensity is

229   best described by the regional context.

230   As highlighted previously, the clear concentration of dune facilitation studies in temperate

231   dunes suggests that we need to expand the scope of coastal dune interaction studies to other geographic

232   regions. This is important for a number of reasons. Macroecological synthesis is an important, novel,

233   and dominant source of theory validation in community ecology (Keith et al., 2012). Alpine and semi-

234   arid syntheses (Maestre, Valladares & Reynolds, 2005; Arredondo-Núñez, Badano & Bustamante,

235   2009) and large-scale integrated experiments (Fraser et al., 2013) are a powerful means to test global

236   issues including the importance of small-scale processes (Paine, 2010) such as interactions.

237   Considering that coastal dunes are subject to significant global change effects (van der Meulen, Witter

238   & Ritchie, 1991), understanding how plant interactions vary between geographic regions increases

239   predictive ecology on important issues such as climate change effects on plant community structure

240   globally (Michalet et al., 2014). As highlighted by Hesp (2004), even though few comparative studies

241   have been carried out, differences in factors such as species, adaptative strategies and rates of plants

242   growth indicate that ecological processes may be distinct between tropical and temperate dunes in

243   many systems.

244   Another major limitation identified by the systematic review was the predominance of

245   observational studies over experimental studies. Observational studies included spatial association

246   analyses among species (McIntire & Fajardo 2009; Cushman, Waller & Hoak, 2010; Castanho,

247   Oliveira & Prado 2012). Although positive associations provide evidence of facilitation, this

248   associational pattern does not exclude alternative explanations such as shared physical microhabitats

249   requirements and the tendency of some plants to act as foci for seed deposition (Callaway 1995).

250   Alternatively, experimental manipulations provide a causal form of verification for plant facilitation

251   because the mechanistic pathways can be identified (Callaway 2007). Consequently, we also

252   recommend that coastal dunes be studied more comprehensively using manipulative approaches or a

253   combination of observational and experimental methodologies to decouple direct from indirect effects

254   (Kunstler et al., 2006), identify mechanisms (Shumway, 2000; Maestre, Bautista & Cortina, 2003;

255   Cushman, Lortie & Christian, 2011), and examine the importance of local variation (Lu et al., 2011;

256   McIntire & Fajardo, 2014). The extent that facilitation or plant interactions in general can be used to

257   manage or restore highly impacted/stressed systems such as coastal dunes is generally best examined

258   through manipulation.

259   The quantitative examination of plant facilitation magnitude across studies, i.e. the meta-

260   analyses, showed that the factors influencing the occurrence and magnitude of facilitation in coastal

261   dunes depended on the response variable measured. Whilst geographical region influenced the

262   magnitude of facilitation for plant growth and survival, no effect of region was observed on

263   interactions regarding plant density (Table 2). This result supports the general findings of another

264   meta-analysis on facilitation for arid and semi-arid environments that concluded that the effect of

265   abiotic stress on the outcome of interactions depended on the plant response (Maestre, Valladares &

266   Reynolds, 2005). In order to explain this difference between response variables, we need to better

267   understand how the neighbor presence changes the conditions and resources in its neighborhood and

268   how it affects the distinct species-specific responses (Michalet et al. 2014). Therefore, to better

269   understand the factors affecting the magnitude of positive interactions, we must investigate the

270   mechanisms behind facilitative interactions in coastal dunes and importantly also record multiple target

271   responses to neighbors (Hastwell & Facelli, 2003; Brooker et al., 2008). This is rarely done in a single

272   study (but see for instance Rudgers & Maron, 2003; Cushman, Lortie & Christian, 2011) but is

273   nonetheless an important avenue of research that will benefit assessment of restoration efforts.

274   Growth and survival trends suggest that geographic region mediates the presence of facilitation

275   more broadly in coastal dune systems. This is a very novel finding (Thebault et al. 2014). Altogether,

276   these results showed that the presence of a neighbor was positive for plant survival and growth in the

277   tropical region, whereas in the temperate and subarctic regions, the effects were neutral for both plant

278   response variables. The environmental severity is relative to the stress tolerance and resource use

279   adaptations of the species within a system (Lortie, 2010). The species composition and predominant

280   life-forms differ between tropical and temperate dunes (Hesp, 2004). Therefore, the observed result can

281   be the product of different sets of traits associated with the species in each region respectively, and

282   consequently, distinct sensitivities to the changes in conditions and resources generated by neighbor

283   presence in the tropical and temperate dunes. However, the limited number of tropical studies indicates

284   that we need to be cautious in the generalization of this alternative hypothesis at this junction. In the

285   present synthesis, we focused on only facilitation studies to test hypothesis related to the magnitude of

286   this interaction, although competition and facilitation are of course both subsets of plant-plant

287   interactions. To explore and contrast the relative importance of competition and facilitation, primary

288   studies in coastal dunes must now test them directly and concurrently and the scope of a synthesis must

289   be expanded including also plant competition studies.

290   The capacity for regional drivers of change to mediate positive, local interactions is a novel and

291   important challenge to traditional community ecology and suggests that studies must also now consider

292   the regional context in studying plant-plant interactions even at relatively fine scales in these systems.

293   From a restoration and management perspective, this also suggests that best practices in using

294   facilitation to reduce potential anthropogenic or disturbance effects may need to be tested and/or

295   applied via different mechanistic pathways depending on the importance of regional drivers on

296   productivity gradients and specific local limitations to key target plant species.

297   The use of remote sensing data together with meta-analytical techniques could be a powerful tool

298   to explore the importance of climatic and environmental covariates (usually not provided by primary

299   studies) driving ecological processes. In the present study we did not find an effect of NDVI and MAP

300   on the variability of plant interaction in coastal dunes. One possible explanation for the failure to detect

301   a significant effect of the remote sensing covariates and the other local covariates also tested (plant life-

302   form and life-stage) is the highly variable nature of ecological data together with the small number of

303   primary studies available to construct a big picture. However, as we accumulate primary data testing

304   plant facilitation in coastal dunes, we should be able to drawn synthesis with more definitive

305   conclusions about the factors driving facilitation intensity.

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Prisma flow diagram.

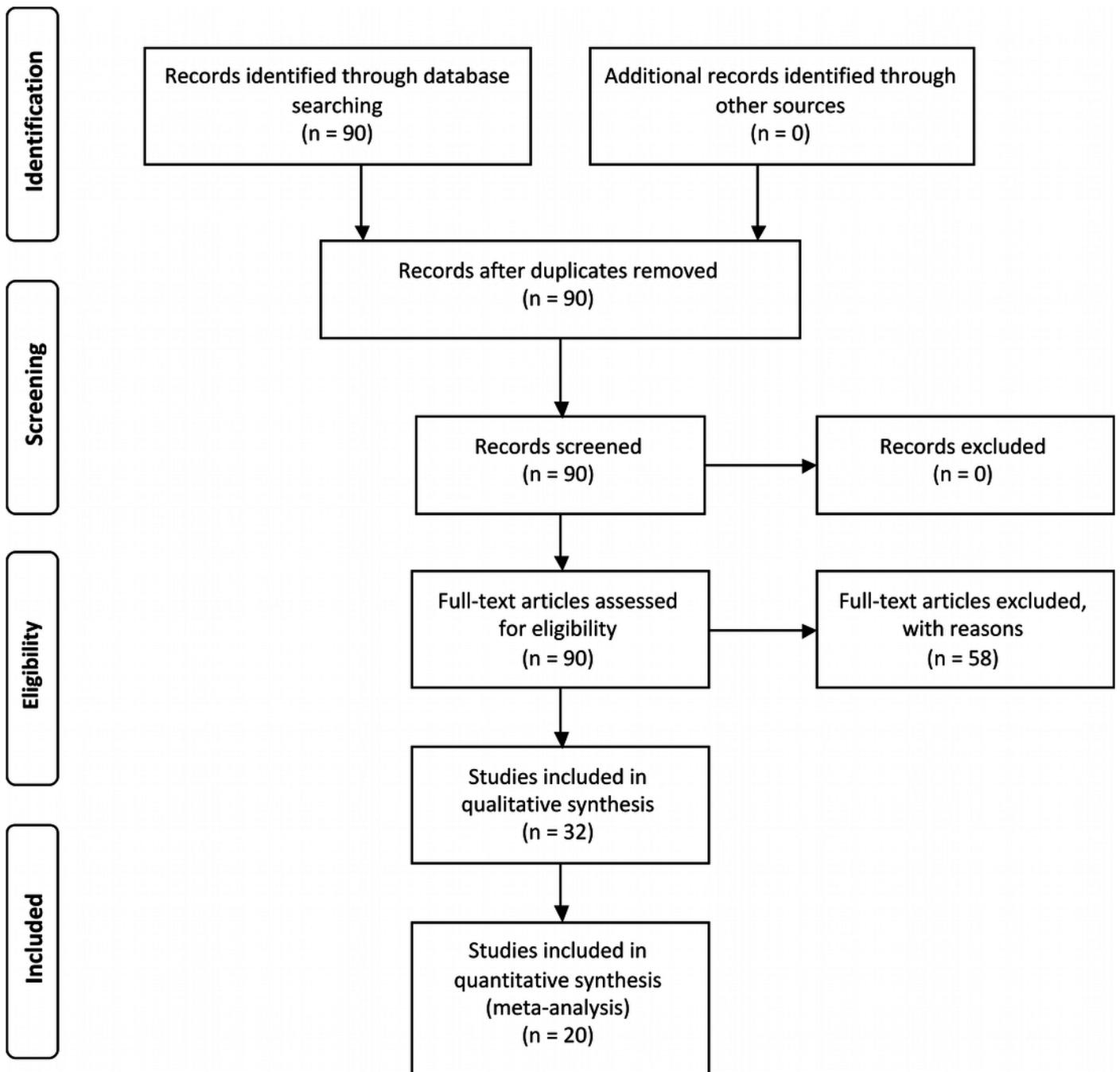
Figure 1. Prisma flow diagram depicting the seach protocol and workflow in determining the effective population of studies for systematic review and meta-analysis.

Meta-analysis studies.

Table 1. The total number of suitable independent cases for meta-analysis (outcomes) and the respective total publications for each plant response variable studied in coastal dune systems globally. The WoS search tool was used to populate the list of studies used.

PERFOMANCE	N CASES	N PUBLICATIONS
Density	40	10
Growth	39	10
Survival	42	8
Richness	17	4
Reproductive output	10	4
Emergence	4	2
Occurrence	8	2

Summary of meta-analyses results.

Table 2. Summary of the random effect models used to examine the key factors on plant neighbor effects for plant density, growth, and survival in coastal dune systems. DF= degrees of freedom; R^2= proportion of the true variation explained by the independent variable; Slope= only applicable for continuous predictors.

	EFFECT	DF	R^2 (%)	SLOPE	P
	Geographic region	2,37	0.7	---------	0.33
	MAP	1,38	0.0	-0.0003	0.67
	NDVI - regional	1,38	0.0	-0.124	0.49
Density	NDVI - local	1,27	0.0	1.070	0.54
	Neighbor life-form	2,37	0.0	---------	0.98
	Target life-form	3,36	0.0	---------	0.88
	Target life stage	2,37	0.0	---------	0.69
	Geographic region	2,36	20.0	---------	**0.03**
	MAP	1,37	0.0	0.001	0.13
	NDVI - regional	1,36	0.0	-0.030	0.70
Growth	NDVI - local	1,15	0.0	-0.136	0.95
	Neighbor life-form	1,37	0.0	---------	0.62
	Target life-form	1,37	0.0	---------	0.40
	Target life stage	2,36	17.5	---------	0.08
	Geographic region	1,40	17.1	---------	**0.03**
	MAP	1,40	0.0	-0.001	0.40
	NDVI - regional	1,40	0.0	-0.113	0.29
Survival	NDVI - local	1,28	0.0	-1.646	0.30
	Neighbor life-form	2,39	0.0	---------	0.15
	Target life-form	2,39	0.0	---------	0.36
	Target life stage	1,34	9.2	---------	0.19

Mean effect sizes by geographical region, and the overall effect for plant growth and survival, in coastal dune systems.

Figure 2. Mean effect sizes by geographical region, and the overall effect for A) plant growth and B) plant survival, in coastal dune systems. Error bars are bias-corrected bootstrap 95% confidence intervals. The number of independent cases (outcomes) is shown in parentheses. Across all study cases, the presence of neighbor had a positive effect on overall growth but no effect on survival of the target species (given that confidence intervals that do overlap zero). Geographic region explained a portion of the variability among study cases (20% of target growth and 17% of survival). Although the small number of cases in the tropical region, neighboring plants increases the growth and survival of target plants in the tropics (confidence interval do not overlap zero), while no effect was observed in the temperate region and subartic (the last just in the case of growth).