Ecology and evolution of invasive plants: what to study next?

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In recent decades, a growing number of studies have addressed connections between ecological and evolutionary concepts in biologic invasions. These connections may be crucial for understanding the processes underlying invaders' success. However, the extent to which scientists have worked on the integration of the ecology and evolution of invasive plants is poorly documented, as few attempts have been made to evaluate these efforts in invasion biology research. Such analysis can facilitate recognize well-documented relationships and identify gaps in our knowledge.

We applied the network approach to the representation of current research on the ecology and evolution of invasive plants in the family *Poaceae*. We restricted our study to empirical articles and used the *Web of Science* ® advanced search tool to compile the number of articles that explicitly addressed pairs of nodes in the field tag "topic", i.e. the title, abstract and keywords.
An initial universal search (#1) attempted to restrict the results to publications about exotic *Poaceae*: "TS=(grass OR Poaceae) AND TS = (invasi* OR introduced OR exotic OR non-indigeneous OR nonindigeneous OR alien) ".
A search syntax was then established for each node, including the keywords determined for each concept (Table 1). For instance, the node *"phenotypic and trans-generational plasticity"* was searched with the syntax : "#1 AND TS=(Plastic* OR "general purpose genotype" OR "reaction norm" OR "maternal effects" OR "carry-over effects" OR "transgenerational plastic*".
The 18 node searches (#2 to #19) were then combined in pairs. The number of published articles listed for each of the 153 pairs of nodes was compiled in a raw matrix for network analysis. A second, verified matrix was compiled, comprising the number of articles remaining after the 153 pairwise concept lists were hand-checked to discard irrelevant articles. Relevance was determined by reading the title, abstract and keywords. Additionally, only empirical studies that explicitly addressed the pertinent concepts in an exotic plant from the family *Poaceae* were kept.
Network representations (Fig. 1) of research in the ecology and evolution of exotic *Poaceae* were generated using both raw and verified matrices, using Ucinet ® software.

Table 1. Conceptual nodes used in the network visualization and corresponding keywords for literature searches.

Nodes	Related keywords
Time scale of invasion	Time, temporal scale, speed, periodicity, frequency
Dispersal and spatial scale of invasion	Dispersal, terminal velocity, colonization, colonisation, long-distance dispersal, dispersal corridor, migration, spatial scale, geographic pattern, species' range, geographic range, native range, invasive range, range expansion, spread, foci, landscape
Demography	Demography, demographic process, demographic swamping, abundance, propagule pressure, density, density-dependence, Allee effect, aggregation
Plant development	Plant development, propagule size, seed morphometrics, germination, emergence , establishement, seedling, growth, development, resource allocation, biomass, plant height, morphological variation, morphology, trait, phenology
Reproduction	Reproductive success, reproduction, reproductive output, seed production, seed number, fruit, flower, flowering, pollen, mate availability, mating, crossing, reproductive strategies, life history strategies, annual, perrennial , perrenniality, clone, clonal, asexual, sexual, agamospermy, apomixy, apomixis, vegetative reproduction, parthenogenesis, breeding system, reproductive system, autogamy, autogamous, allogamy, allogamous, selfing, outcrossing, self-incompatibility, self-compatibility, unisexual, bisexual, inbreeding
Ecological niche	Ecological niche, niche, habitat specificity, ecological range, functional group, guild
Biotic interaction	Biotic interaction, biotic resistance, allelopathy, competition, mutualism, symbiotic interactions, symbiose, symbiosis, plant-animal interaction, plant-insect interaction, herbivory, herbivore, pollination, pollinator, mycorrhizae, pathogen, fungi, bacteria, disease, succession, facilitation, inhibition, tolerance, keystone species
Environmental conditions	Environment, conditions, gradient, climate, altitude, latitude, soil, nutrient, soil, water, holding capacity, hydrology
Human influence	Human influence, human-induced disturbance, anthropogenic change, global change, global warming, climate change, anthropogenic change, fire, ruderal, agriculture, tillage
Plasticity	Plasticity, phenotypic plasticity, plastic response, general purpose genotype, reaction norm, maternal effects, carry-over effects, transgenerational plasticity
Genetic diversity	Genetic structure, genetic architecture, genetic diversity, genetic variation, genetic variance, phylogeny, quantitative trait loci, genome, genomic rearrangements, genomics, polymorphism, chromosome structure
Epigenetics	Epigenetics, methylation
Ploidy	Ploidy, polyploidy, allopolyploidy, autopolyploidy, ploidy level, chromosome counts, chromosomes numbers, tetraploidy, hexaploidy, octoploidy, cytotype
Hybridization	Hybridization, hybrid, genetic swamping, genetic deterioration, genetic takeover, genetic aggression, genetic assimilation, introgression
Mutation	Mutation, mutant
Stochastic population differentiation	Stochastic population differentiation, stochastic process, genetic drift, founder effect, inbreeding, inbreeding depression, outbreeding depression
Deterministic population differentiation	Deterministic population differentiation, population differentiation, adaptation, adaptive evolution, adaptive process, adaptive divergence, adaptive radiation, fitness, selection, coevolution, niche shift, niche displacement, speciation
Gene flow	Gene flow, metapopulation, pollen movement, source and sink

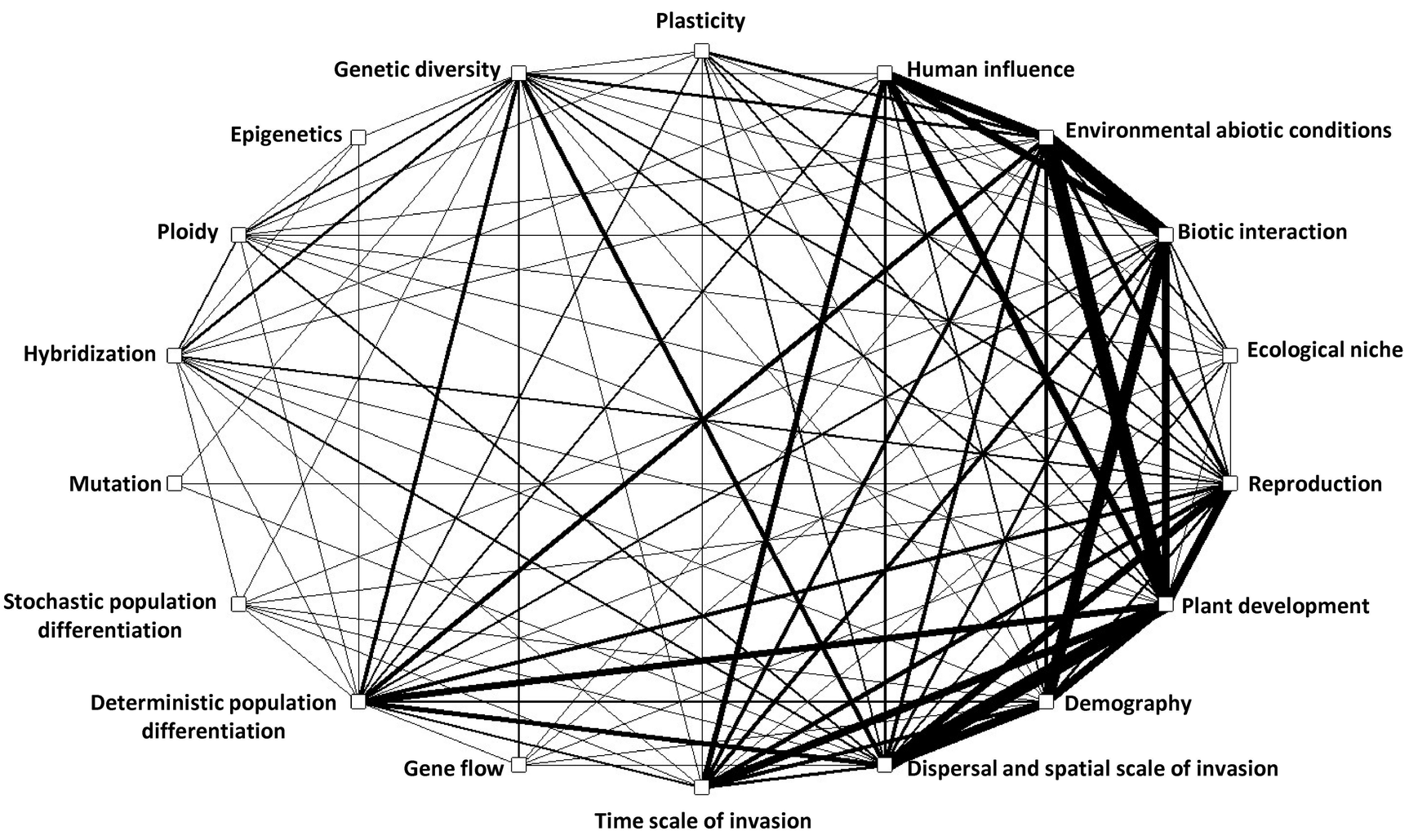

Fig. 1. Example network, representing research connecting ecological and evolutionary concepts in exotic Poaceae *grasses. Edge thickness represents the number of published articles (referenced in Web of Science ®) that connect two concepts after abstract verification to discard irrelevant articles.*

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Take-home message

Identified research questions include:

- What is the importance of plasticity in an invader's response to human-induced disturbance? *(human influence x plasticity)*
- What is the relationship between patterns of gene flow and the temporal dynamics of invasion? *(time scale of invasion x gene flow)*
- Do polyploids have higher invasiveness in humandisturbed environments? *(human influence x ploidy)*
- How do human activities affect gene flow in invading populations? *(human influence x gene flow)*
- Do epigenetic mechanisms allow invasive species to display increased phenotypic plasticity? *(plasticity x epigenetics)*