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Experimental Evidence from Causal Criteria Analysis for the Effects of Common Carp *Cyprinus carpio* on Freshwater Ecosystems: A Global Perspective

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As the most widely distributed freshwater fish worldwide, common carp Cyprinus carpio *can be either invasive or "naturalized" in most areas of introduction. This leads to different levels of perception regarding the species' role in freshwater ecosystems, with experimental research focusing either on its "middle-out" impacts or overall function in limnological processes. At the same time, the large scales at which carp dynamics operate may severely limit the validity of laboratory and, oftentimes, field experiments in extrapolating results to real-world ecosystems. In this study, 129 laboratory, field, and "natural" experiments were systematically reviewed through causal criteria analysis, and within an historical/biogeographical and risk-assessment context. Of the 19 countries where experiments were conducted, only 4 were considered as "low risk" and one as "no risk," the other being "medium" to "high risk." Experimental findings from 373 component-wise assessments supported the framework of effects on water quality, vegetation, invertebrates, and vertebrates, with the latter including also amphibians and waterfowl, previously unreported. Stronger evidence was provided by natural and field relative to laboratory experiments, reflecting the reductionism of the latter. Critical biomass for an impact was highly dependent on experimental setup, even though the overall threshold of ≈200 kg ha^{-1} under natural conditions supported recent findings. Management of carp should reflect the level of current and potential risk posed by the species in its different areas of distribution, thereby accounting for projections of further spread but also for unsuccessful colonization. Future experimentation should favor a holistic→reductionist over a reductionist→holistic approach.*

Keywords Field, Laboratory, Natural, Enclosure/exclosure, Biomass

INTRODUCTION

The common carp (*Cyprinus carpio*, Cyprinidae; hereafter, "carp") has long been regarded as a highly invasive and noxious non-native species worldwide, but especially in North America (McCrimmon, 1968; Moyle, 1984) and in Australia (Koehn, 2004), with localized impacts identified more recently in several other parts of the species' introduced range (see Vilizzi, 2012). The management of carp has therefore become a priority issue in efforts to mitigate the species' detrimental effects on freshwater ecosystems (Britton et al., 2011b). This is especially true for ecosystems already degraded by human disturbance (e.g., Smith et al., 2009) and those vulnerable to the effects of climate change (e.g., Britton et al., 2010). The carp is able to colonize these ecosystems by virtue of its generalist ecological requirements (Balon 1974, 2004), and

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ultimately the consequences of carp invasion are a decrease in native biodiversity and concurrent homogenization of the fish fauna (Marr et al., 2013). Mitigation of these impacts results in costly eradication and control measures (whenever feasible) as well as economic losses due to a deterioration in amenity value (e.g., Koehn et al., 2000).

Conversely, in other parts of its introduced range (e.g., central Europe), the carp may be accepted as a "naturalized" species (i.e., long-established, self-sustaining populations: Copp et al., 2005) that poses little or no threat to the environment (e.g., Arlinghaus and Mehner, 2003; Szücs et al., 2007). The carp is also valued in some areas as a food stuff (Balon, 2004; Britton et al., 2010) or as a much prized angling amenity (Britton et al., 2010; Brazier et al., 2012). Whereas, in still other naturalized areas, such as Western Europe and Thrace/Anatolia (Turkey), the carp's status is being re-assessed. This is due to increasing awareness of the potential risks posed to native biota (Almeida et al., 2013; Copp et al., 2015a; Tarkan et al., 2014). despite the species' long culinary tradition (Spates 2013) and commercial value (e.g., Turkish Statistical Institute, 2012),

In a representative review of the relevant literature, the mechanisms behind the carp's effects on the aquatic environment were reported to involve the simultaneous alteration of bottom-up and top-down processes through a "middle-out" framework (Weber and Brown, 2009). Accordingly, the carp's resuspension of bottom sediments during benthic foraging leads to: (i) increases in turbidity, nutrient levels (also through excretion mainly by 0+ individuals) and phytoplankton production; (ii) reductions in benthic invertebrate abundance, diversity, and richness (also by direct feeding); and (iii) the uproot of aquatic macrophytes (sometimes also consumed directly). Increased levels of turbidity, nutrient, and phytoplankton negatively affect: aquatic macrophyte growth through shading and smothering, benthic invertebrates by clogging of attachment sites, and zooplankton by altering community structure. These direct and indirect effects ultimately follow (alternative equilibrium theory: Scheffer et al., 1993), causing most shallow-lake ecosystems to switch from a macrophyte-dominated, clear-water (oligotrophic) state to a phytoplankton-dominated, turbid-water (eutrophic) state. The resulting degraded habitat conditions negatively affect the abundance and richness of native fishes (mainly piscivores and sight predators), and severely compromise amenity values (e.g., sport fishing and tourism industry).

Yet, despite the large number of experimental studies supporting the above framework, the relevance to community and ecosystem ecology of experiments conducted at spatial and/or temporal scales inappropriate for the processes and organisms under investigation has been questioned (Carpenter, 1996). In the present context, this argument applies to the extrapolation of findings from laboratory or field experiments to the "real-world" freshwater ecosystems. At the same time, the seemingly contrasting perspectives provided by so-called "ecology-in-ecosystem" vs. "ecology-of-ecosystem" approaches (Carpenter, 1999) may ultimately reflect a "harmonic duality" (cf. Balon, 1988). This is because development of models across a range of spatial scales and levels of process complexity has been encouraged as a means by which to understand the regulating processes of aquatic ecosystems (Huston, 1999)—an essential requirement for more robust inference (Diamond, 1983).

Similar to "migration, wolves, and salmon," carp are likely to be "too large, wide ranging" (Carpenter, 1996: p. 678) to be constrained within the boundaries of experimental microcosms and/or mesocosms (*sensu* Odum, 1984). This is a crucial aspect if reliable and holistic conclusions are to be drawn on the effects of carp on freshwater ecosystems. Indeed, carp population dynamics are known to operate at large spatial scales (Otis and Weber, 1982; Nicol et al., 2004; Penne and Pierce, 2008; Jones and Stuart, 2009; Butler and Wahl, 2010; Daniel et al., 2011). The adult carp aggregate in the deeper areas of river channels and lakes during the colder months (Johnsen and Hasler, 1977; Cooke and McKinley, 1999; Brown et al., 2000, 2001; Bajer et al., 2011; Taylor et al., 2012) and during the warmer months they undertake spawning migrations toward shallow, heavily vegetated backwaters and floodplain areas (Rodriguez-Ruiz and Granado-Lorencio, 1992; Taylor et al., 2012). Similarly, age-0 carp undergo dispersal movements out of their "nursery grounds" after reaching a critical size and/or stage of development (Reynolds, 1983; Vilizzi and Walker, 1999; Stuart and Jones, 2006). The carp's worldwide distribution is remarkable, with self-sustaining populations established in 91 of 120 countries where the species was introduced (Welcomme, 1988; Casal, 2006), encompassing diverse climatic regimes (i.e., tropical, arid, temperate, and cold: Peel et al., 2007), both lotic and lentic habitats in fresh-to-brackish waters (e.g., Balon 1995, 2004; Whiterod and Walker, 2006) as well as various political and socio-economic circumstances (cf. Balon, 1995; Vilizzi, 2012). As such, the ubiquity of carp limits the scope of reductionist approaches such as those typical of controlled experimental conditions.

To date, most reviews of carp effects on freshwater ecosystems have been conducted in a "narrative" (*sensu* Webb et al., 2013) or, at best, semi-quantitative format. Apart from the more extensive review by Weber and Brown (2009), which evaluated 37 controlled experiments and 23 management-oriented studies, other reviews have summarized information from representative samples of experiments (e.g., Chumchal and Drenner, 2004; Chumchal et al., 2005; Petr, 2000; Hertam, 2010) or focused on experimental research specific to a certain area of carp distribution (e.g., McCrimmon, 1968; King, 1995; Vilizzi, 2012). Exceptions are the quantitative meta-analyses of Matsuzaki et al. (2009a), who reviewed 16 studies satisfying certain criteria for inclusion for the detection of significant effects, and of Kulhanek et al. (2011), who were able to incorporate 30 studies in total into their predictive model(s) that related carp biomass and preimpact conditions to level of impact severity. In general, the strength of "systematic" (*sensu* Webb et al., 2013) over "narrative" reviews is that the former allow the synthesis of literature information on one or more research questions as well as the testing of hypotheses to provide insights beyond those achievable through a qualitative

(or semi-quantitative) assessment of individual studies. In this respect, recent developments in the application of evidence-based, causal criteria analysis to environmental management studies have provided ecologists with a powerful tool for quantifying (putative) cause–effect linkages (Norris et al., 2012).

To synthesize nearly nine decades of research conducted at the worldwide scale, the aim of the present study was to undertake a global review and meta-analysis of experimentation on the effects of carp on freshwater ecosystems, including the uncontrolled experimental studies not included in previous reviews (i.e., Weber and Brown, 2009; Matsuzaki et al., 2009a). The specific objectives were to: (i) evaluate the largest possible collection of experiments (as retrievable from the published literature) according to "setup" (i.e., location, size of arena, and plot type) and within a historical and biogeographical context; (ii) assess the relevance of carp negative effects (i.e., impacts) on a total of ten ecological components in terms of (country-specific) risk levels based on carp status, invasiveness, and degree of public perception and scientific concern; (iii) revisit existing conceptual models of carp effects on freshwater ecosystems in the light of the additional findings from the present study; (iv) discuss issues related to biomass threshold identification; and (v) provide recommendations for the direction of future experimental research by highlighting the importance of implementing a holistic→reductionist approach rather than a reductionist→holistic approach.

METHODS

Components

To evaluate the effects of carp on freshwater ecosystems, 10 abiotic and biotic ecological components were investigated. Abiotic components included: turbidity/solids, nitrogen, and phosphorus; biotic components included phytoplankton/chlorophyll *a*, aquatic macrophytes, zooplankton, benthic invertebrates, amphibians, waterfowl, and fish. Notably, "nutrients" were split into nitrogen and phosphorus (but without further distinction: e.g., Matsuzaki et al., 2009a), as the effects of carp on these components were sometimes found to be at variance with each other. Whereas, no distinction was made between "large" and "small" zooplankton, as this was found to depend on the taxa examined and/or the approach adopted in a certain study, hence not suitable for generalization across all reviewed studies.

Experiments

Selection

A "comprehensive" collection of experimental studies of carp effects on freshwater ecosystems was compiled from available, published literature sources, including peer-reviewed papers, thesis dissertations, and in some cases gray literature (i.e., reports). Unlike Weber and Brown (2009) and Matsuzaki et al. (2009a), uncontrolled experimental studies were also included for the sake of completeness (i.e., historical extent) and for the evidence-based evaluation through causal criteria analysis (see below). Using the same criterion as Copp et al. (2009), investigations were included if one or more of the study's components had immediate/eventual application to natural freshwater ecosystems. Thus, studies entirely within an aquacultural context were not included (e.g., Knösche et al., 2000; Kloskowski, 2011a; Adámek and Maršálek, 2013). Also, remaining consistent with the approach adopted by Weber and Brown (2009), control/management-oriented restoration studies, including those providing mitigation of an impact prior to intervention (e.g., Pinto et al., 2005; Bio et al., 2008; Thomasen and Chow-Fraser, 2012), were not included in the present, quantitative meta-analysis.

Categorization

As per Diamond (1983), experiments were first categorized, based on location, as laboratory, field or natural (Table 1). Laboratory experiments were defined as those conducted in a specially designed environment (i.e., aquaria/ponds located in laboratory/outdoor facilities), in which variables can be easily controlled. Field experiments were those carried out in the species' own environment (i.e., semi-natural ponds or natural ponds/water bodies), in which more limited control on the variables of interest is generally possible. Whereas, natural experiments were those in which one or more of the (independent) variables of interest (e.g., carp biomass) vary naturally so that their effects on the response variable(s) (e.g., turbidity and macrophyte cover) can be quantified. Notably, laboratory and field experiments have also been referred to as "manipulative," and natural experiments as "mensurative" (Hurlbert, 1984).

The second level of categorization was applied to laboratory and field experiments according to type of "arena" used, ranging from laboratory experiments to natural water bodies (Table 1). By definition, natural experiments were carried out in a natural water body, and artificial ponds were defined as man-made (e.g., concrete) ponds, generally located at outdoor facilities. Whereas, semi-natural ponds encompassed those fed by a natural river/lake water and/or long-established for human usage. Finally, the plot type used (i.e., enclosures or exclosures: *sensu* Aerts et al., 2009) was also recorded so that enclosure experiments were those in which carp were stocked within a confined space; this contrasted exclosure experiments, which prevented carp from accessing a confined area of water thereby evaluating the species' effects as a "free-ranging" organism. Thus, enclosure experiments included arena types 1–4 and 5–9, and exclosure experiments encompassed types 5 and 11–12 (Table 1).

Based on the above categorization, the reviewed experiments could be arranged along a "reductionism–holism" continuum (cf. Huston, 1999), ranging from a higher level of

Table 1 Categorization of experiments evaluating the effects of carp on freshwater ecosystems

Experimental continuum	Location	Experimental constraints	Arena	Plot type
Generality/realism ↔ Manipulation/control	Laboratory	Low ↔ High	(1) Aquaria	Enclosures
	Laboratory		(2) Enclosures within tanks	Enclosures
	Laboratory		(3) Tanks	Enclosures
	Laboratory		(4) Enclosures within artificial ponds	Enclosures
	Laboratory		(5) Exclosures within artificial ponds	Exclosures
	Laboratory		(6) Artificial ponds	Enclosures
	Field	Low ↔ High	(7) Enclosures within semi-natural ponds	Enclosures
	Field		(8) Semi-natural ponds	Enclosures
	Field		(9) Enclosures within a water body	Enclosures
	Field		(10) Stocked water body	Enclosures
	Field		(11) Exclosures within a water body	Exclosures
	Field		(12) Natural ponds	(Exclosures)
	Natural	None	Natural water body	—

Arrangement is along a manipulation/control and generality/realism continuum based on location of the experiment, with laboratory and field experiments further arranged along a high-low level of experimental constraints continuum depending on type of experimental arena. For each category, plot type is also indicated (after Aerts et al., 2009).

manipulation/control (e.g., laboratory experiments) to a higher level of generality (e.g., field and, especially, natural experiments). In addition, both laboratory and field experiments were arranged along a high–low level of experimental constraints continuum depending on type of arena. Importantly, field experiments carried out in a stocked water body were regarded as less holistic than those in natural ponds or using exclosures (Table 1). This was because, under these experimental conditions, carp densities are inevitably manipulated, even though intended to replicate those believed to be occurring under natural settings. Finally, the proposed arrangement is thought to reflect closely the spectrum of research strategies identifiable in experimental design practice, which according to Kirk (2013) ranges from "experiments" (laboratory) and "quasi-experiments" (field) to "case studies" and "naturalistic observations" (natural experiments).

Studies that dealt with two or more experimental setups were reviewed separately; whereas, in cases where the outcomes of an experiment were published in more than one paper, the corresponding references were listed together. Also, whenever provided in the source study, the surface area of the experimental arena was recorded, or where necessary derived from the stated dimensions and converted into m^2 or ha. Also recorded was the stocked biomass of carp (again, if originally provided) for enclosure experiments, which was otherwise replaced *in lieu* by density of individuals per unit area, or by min–max length or weight of fish, or other measures as per original source.

Evaluation

Component Groups

To evaluate the proportion of experimental locations (i.e., laboratory, field, and natural) and plot types (i.e., enclosures, exclosures, or none, as in the case of natural experiments) used to assess carp effects, the components under scrutiny were combined into four groups: water quality, vegetation, invertebrates and vertebrates (Table 2). Apart from their taxonomic/limnological meanings, these groupings were required for analytical reasons, namely, to achieve appropriate sample sizes and numbers of categories for comparisons to be statistically robust. Similarly, an evaluation was made of the proportion of experimental locations and plot types used to assess carp effects by age-0 (0+), age-1 (1+) and older individuals. Chi-square (χ^2) analysis (http://www.webcalculator.co.uk//x2f91.htm, 16 June 2015) was employed as a test of significance ($\alpha = 0.05$) for contingency tables, except for the Fisher Exact test in one case because of low sample sizes (http://vassarstats.net/fisher2x4.html, 16 June 2015).

Robustness

To quantify the robustness of a laboratory or experiment in terms of setup, level of replication, use of controls and ability to draw conclusions at the appropriate ecosystem scale, an evidence-based weighting system was developed (Table 3): (i) from 0 to 5 for evidence weightings, depending on setup, for both laboratory and field experiments; (ii) 0 or 1, if replication was absent or present, respectively; (iii) 0 or 1, if controls were used or not, respectively; and (iv) from 0 to 3, depending on the strength of conclusions. The latter were categorized as: NO (none: weight = 0), for an experiment that extrapolated results to the ecosystem scale and/or did not address limitations with the findings; CA (caution: 0), for an experiment suggesting caution in interpreting/extrapolating outcomes at the ecosystem scale; BK (back-up: 1), for an experiment that "backed up" the results with those of other experiments conducted at the same and/or different scales (e.g., a laboratory with a field experiment, a field with a natural experiment); SS (same scale: 2), for an experiment conducted at the scale appropriate for the outcomes discussed. In those cases where an

Table 2 Cause–effect hypotheses linking carp (biomass/density) to 10 freshwater ecosystem components (redundancy in Cause section of table is for consistency with causal criteria notation: Webb et al., 2013)

Cause		Effect		Hypothesis	
Organism	Trajectory	Component	Trajectory	In favor	Against
Carp	Increase	(i) Turbidity/suspended solids	Increase	Cc + → TU +	Cc + → TU (0, −, Δ)
Carp	Increase	(i) Nitrogen	Increase	Cc + → N +	Cc + → N (0, −, Δ)
Carp	Increase	(i) Phosphorus	Increase	Cc + → P +	Cc + → P (0, −, Δ)
Carp	Increase	(ii) Phytoplankton/chlorophyll *a*	Increase	Cc + → PH +	Cc + → PH (0, −, Δ)
Carp	Increase	(ii) Aquatic macrophytes	Decrease	Cc + → MA −	Cc + → MA (0, +, Δ)
Carp	Increase	(iii) Zooplankton	Change	Cc + → ZP Δ	Cc + → ZP (0, +, −)
Carp	Increase	(iii) Benthic invertebrates	Decrease	Cc + → BI −	Cc + → BI (0, +, Δ)
Carp	Increase	(iv) Amphibians	Decrease	Cc + → AM −	Cc + → AM (0, +, Δ)
Carp	Increase	(iv) Waterfowl	Decrease	Cc + → WF −	Cc + → WF (0, +, Δ)
Carp	Increase	(iv) Fish	Decrease	Cc + → FI −	Cc + → FI (0, +, Δ)

Components groupings: (i) water quality; (ii) vegetation; (iii) invertebrates; and (iv) vertebrates. Outcomes in favor or against the hypothesis are indicated. Cc = *Cyprinus carpio*; TU = turbidity/suspended solids; N = nitrogen; P = phosphorus; PH = phytoplankton/chlorophyll *a*; MA = aquatic macrophytes; ZP = zooplankton; BI = benthic invertebrates; AM = amphibians; WF = waterfowl; FI = fish. Outcomes: + (increase); − (decrease); Δ (non-directional change, i.e., increase/decrease or one direction, for a sub-set of the component and no change for the other); 0 (no change). See also Figure 1.

experiment fell into two conclusion categories, these were assigned jointly to that experiment, with the following dyads being applicable: NO-BK (weight = 1), BK-CA (1), SS-CA (2), and SS-BK (3).

Table 3 Evidence-based weighting system used for assessing the robustness of a laboratory or field experiment based on setup (i.e., location and plot type: Table 1), replication, control, and strength of conclusions

Study design component	Evidence weight
Set-up	
Laboratory – Aquaria	0
Laboratory – Enclosures – Enclosures within tanks	1
Laboratory – Enclosures – Tanks	2
Laboratory – Enclosures – Enclosures within artificial ponds	3
Laboratory – Exclosures – Exclosures within artificial ponds	4
Laboratory – Enclosures – Artificial ponds	5
Field – Enclosures – Enclosures within semi-natural ponds	0
Field – Enclosures – Semi-natural ponds	1
Field – Enclosures – Enclosures within water body	2
Field – Enclosures – Stocked water body	3
Field – Exclosures – Exclosures within water body	4
Field – Exclosures – Natural ponds	5
Replication	
No	0
Yes	1
Control	
No	0
Yes	1
Conclusions	
NO	0
CA	0
BK; NO-BK; BK-CA	1
SS; SS-CA	2
SS-BK	3

NO = None (findings extrapolated to the ecosystem scale and/or limitations not addressed); CA = caution (caution in interpretation provided); BK = backup (support provided from related experiments at same or different scale); SS = same scale (appropriate scale for interpretation). The additional four conclusion category dyads arising from the reviewed experiments are also indicated.

For each "assessment," i.e., an experiment that evaluates the effects of carp on a certain ecological component, a total evidence weight was computed as the sum of the above four (partial) evidence weights, with possible values ranging from a minimum of 1 to a maximum of 10 (note that the theoretical value of 0 was never achieved and only set as a "null" reference point). Notably, this range of values was chosen so as to match the one used for the causal criteria analysis of natural experiments (see below). For each component, a mean evidence weight from all assessments was then computed. Differences in evidence weights were tested by permutational univariate analysis of variance (PERANOVA) based on a nested design, which included component group (i.e., water quality, vegetation, invertebrates, and vertebrates) as the main factor and the individual components within as the nested factor, and with both factors fixed. Analysis was carried out in PERMANOVA+ v1.0.1 for PRIMER v6.1.11 (Anderson et al., 2008) following normalization of the data, using a Euclidean distance and 9999 permutations of the residuals under a reduced model (Anderson and Robinson, 2001), and with statistical effects (including *a posteriori* pair-wise comparisons, in case of significance) evaluated at $\alpha = 0.05$. Briefly, the advantage of PERANOVA compared to traditional parametric analysis of variance is that the stringent assumptions of normality and homoscedasticity, which proved very often unrealistic when dealing with ecological datasets, are "relaxed" considerably.

Effects

For each ecological component, the percentage of assessments that found an increase, a decrease, a "change" or no effect of carp was computed. Notably, "change" included either a combined "increase," "increase/no effect", or

"decrease/effect" on a certain component. This prevented further splitting of effects within a certain component, which would contradict definition of the same (e.g., for zooplankton different taxon-specific effects would involve taxon-specific splitting of that component).

Risk Areas

From the available literature, the countries in which experimental studies originated were categorized into risk areas based on the following criteria: carp status, invasiveness, public perception, and scientific concern. Accordingly, carp status was categorized into: "native" (Froese and Pauly, 2014; see also Chistiakov and Voronova, 2009), "semi-native" (i.e., native to some areas of the study country but translocated elsewhere), "naturalized" (*sensu* Copp et al., 2005) or "alien" (i.e., introduced in relatively recent times, established, and invasive), with the latter term preferred over "non-native" in the present context to emphasize the degree of perception about the species' invasiveness and noxiousness. Carp invasiveness was categorized according to the number of invaded areas into: "none," "low," "moderate," and "high." Public perception into: "positive" (e.g., cultural, historical, and sport fishing value), "indifferent" (e.g., mostly unnoticed, public awareness still lacking), and "negative" (e.g., undesired, unpalatable, and "vermin"). Scientific concern (based on the number of reports on documented impacts) into: "none," "low," "moderate," and "high."

For each of the above criteria, a score was assigned to each corresponding category ranging from 0 to 3 (status, invasiveness, scientific concern) or 0 to 2 (public perception), in the order of the above categories. For each country, an outcome score was then computed as the sum of the corresponding partial scores, allowing categorization into four types of risk areas: "no risk" (outcome score = 0), "low risk" (1–4), "medium risk" (5–8), and "high risk" (9–11).

Based on the above-defined risk areas, the number of experiments and assessments were evaluated based on component groups. Because of the different number of countries in the different risk areas, the total number of experiments for each risk area was divided by the number of countries therein to obtain a relative number of experiments. A similar procedure was followed for the total number of component groupwise assessments (except for the no-risk area, because of only one assessment), which was rounded to the nearest integer and the resulting contingency table (i.e., component group vs. risk area) was then subjected to χ^2 analysis.

Cause–effect Relationships

The Eco Evidence approach (Norris et al., 2012; Webb et al., 2013), which is a form of causal criteria analysis adapted to the environmental sciences, was used for weighting and combining evidence from the reviewed experiments on carp effects on freshwater ecosystems. Briefly, the Eco Evidence framework involves eight steps grouped as: (i) problem formulation (steps 1–4 and 6), (ii) literature review and evidence extraction (step 5), and (iii) weighting evidence and judging causation (steps 7 and 8). The process starts with a documentation of the nature of the problem (step 1); proceeds to identify the context in which the problem will be assessed (step 2); develops a conceptual model (step 3); identifies the relevant cause–effect hypotheses (step 4); searches and reviews the literature and extracts evidence (step 5); revises the conceptual model and previous steps, if necessary (step 6); catalogues and weighs the evidence (step 7); and, ultimately, assesses the level of support for the hypotheses, thereby making a judgment (step 8).

Following this framework (Figure 1), the effects of carp on the ten freshwater ecosystem components under investigation (step 1) were to be quantified for inland waters outlined in Table 1 (step 2). The conceptual models of Koehn et al. (2000) and Weber and Brown (2009) were used to define cause–effect relationships, with the former model regarded as more applicable to "other native fauna," including amphibians, waterfowl and fish (Table 2), of which only fish were included in Weber and Brown's (2009) model (step 3). Ten cause–effect hypotheses in total addressed possible effects of increases in biomass of carp (including its presence relative to unaffected areas) on each of the ecological components (Table 2) (step 4). Finally, the evidence provided in support consisted of the reviewed experiments (step 5). For weighting evidence (step 7), two different systems were used for laboratory and field vs. natural experiments. Thus, for laboratory and field experiments, the above-described weighting system for quantification of robustness (Table 2) was used. This was because of the intrinsic structure of these experiments, which would not immediately fit into the Eco Evidence-based weighting system tailored to natural experiments for the monitoring of ecological impacts (Norris et al., 2012). Conversely, the weighting system of the Eco Evidence framework was applied to the natural experiments, which were evaluated according to: study design, number of control/reference locations and number of impact locations (for corresponding weights, see Table 3 in Norris et al., 2012).

Implementation of causal criteria analysis for laboratory and field experiments was in Excel using a customized spreadsheet; whereas, the desktop Eco Evidence v1.1.1 analyzer software (Nichols et al., 2011) was employed for the natural experiments. In both cases, each "evidence item" (= assessment) was assigned an overall evidence weight according to the corresponding weighting system used (i.e., robustness or Eco Evidence based). For each of the 10 hypotheses, the resulting weights were summed for all evidence in favor of the hypothesis and for all evidence against the hypothesis. Following Webb et al. (2013), the two resulting sums were then compared to a threshold value of 20 points, resulting in one of four conclusions for each hypothesis (Table 4). Further, because of the "location" distinction in

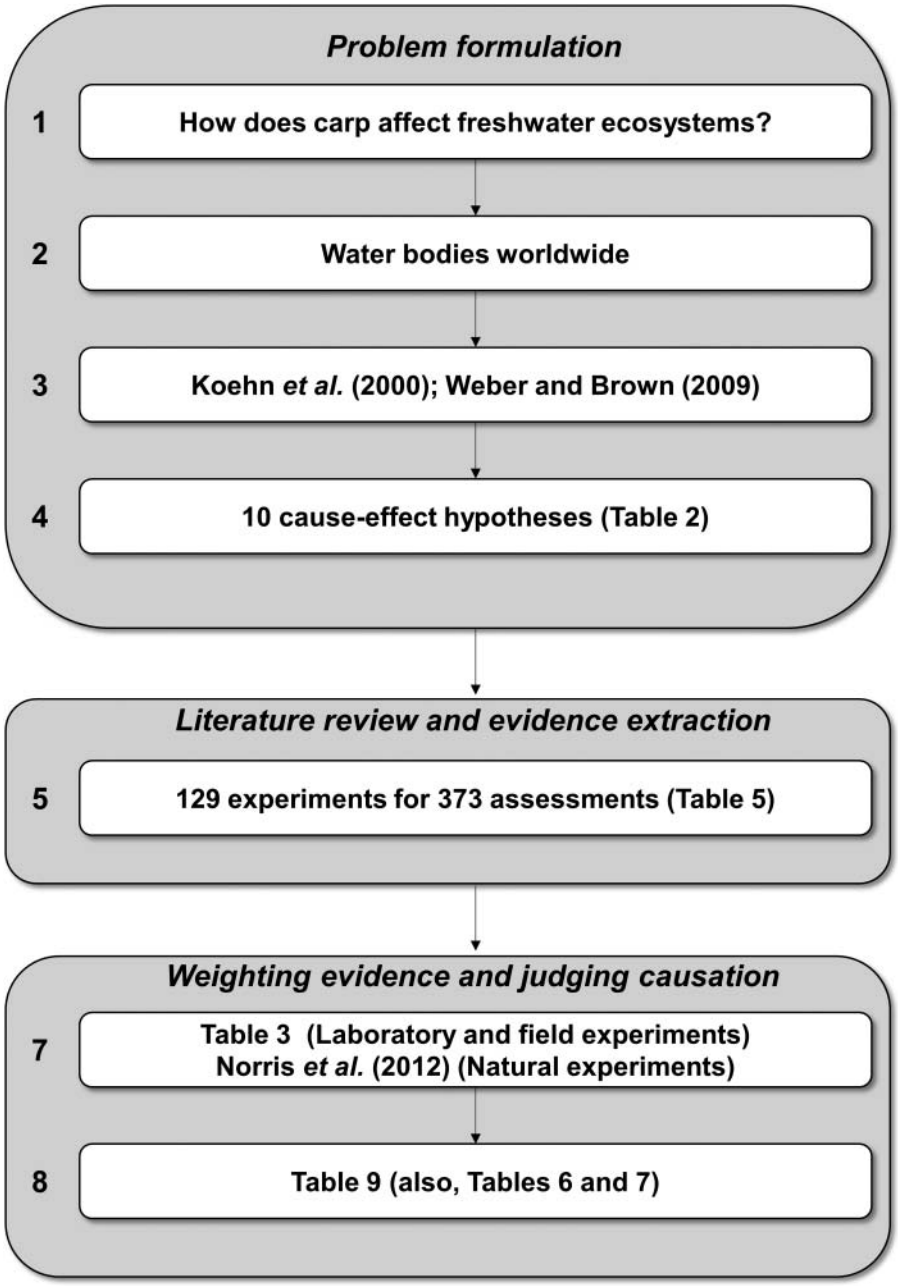

Figure 1 Eco Evidence framework (after Norris et al., 2012) used for weighting and combining evidence from 129 reviewed experiments on carp effects on freshwater ecosystems (see Table 5). Numbers indicate the steps in the process (note that step 6 for "revision" is not included here as the present framework refers to the final conceptual model).

the present study (Table 1), a weight was assigned to each combination of causal criteria analysis conclusion according to location of experiment, resulting in a 3 × 3 matrix (Table 4). Based on this weighting system, an outcome score for each of the 10 components was computed as the sum of the weights assigned across the three types of experiments, with possible values ranging from −6 (i.e., a component for which all types of experiments would support the alternative hypothesis) to 6 (i.e., a component for which all types of experiments would support the hypothesis).

Importantly, to assess the level of support for the ten hypotheses, and therefore pass judgment (step 8 in the Eco Evidence framework), an "impact" refers hereafter to a "quantifiable negative effect" (after Gozlan, 2008). This equates to: (i) an increase in (the concentration of) turbidity/suspended solids, nitrogen, phosphorus, phytoplankton/chlorophyll *a*; (ii) a decrease in (the abundance of) aquatic macrophytes, benthic invertebrates, amphibians, waterfowl, and fish; and (iii) a "variation" (i.e., increase, decrease, or change) in zooplankton composition (i.e., abundance), with

Table 4 Possible conclusions reached through causal criteria analysis on the effects of carp on 10 freshwater ecosystem components (Table 2)

Conclusion		Location of experiment		
Description	Criterion	Laboratory	Field	Natural
Support for hypothesis	≥ 20 in favor, < 20 against	1	2	3
Inconsistent evidence	≥ 20 in favor, ≥ 20 against	0	0	0
Insufficient evidence	< 20 in favor, < 20 against	0	0	0
Support for alternative hypothesis	< 20 in favor, ≥ 20 against	−1	−2	−3

Criteria based on a threshold value of 20 points (after Webb et al., 2013). Depending on location of experiment (Table 1), a matrix of weights is provided to compute an overall outcome score for each of the components under investigation.

increase, decrease and change into variation pooled due to the different documented responses of zooplankton to carp presence (Weber and Brown, 2009).

Biomass

Whenever possible, the biomass at which carp was found to have an impact on an ecological component was recorded. Following normalization of the data, PERANOVA+ was used to test for differences in the estimated mean critical biomass (i.e., at which an impact occurred) amongst component groups (and individual components therein), location of experiment and fish age; using an Euclidean distance, 9999 permutations of the residuals were run under a reduced model, with statistical effects (including *a posteriori* pair-wise comparisons) evaluated at $\alpha = 0.10$ for heuristic purposes and because of the low sample sizes (Kline, 2013). The design was an unbalanced "nested-factorial" with factors Group, Experiment and Age crossed, factor "Component" nested within "Group," and all factors fixed. However, testing was made only for the main effects (hence, disregarding any interactions) because of highly unequal sample sizes, which would have resulted in too many missing cells lowering the power of the tests.

Finally, to obtain an even more realistic estimate of critical biomass, only biomass values from experiments carried out with "free-ranging" carp, i.e., field experiments using exclosures and natural experiments, were considered. Differences amongst component groups and amongst/between the individual components therein were tested based on a nested design analogous to that used for evidence weights, and with similar analytical procedures.

RESULTS

In total, 129 experiments from 119 studies were reviewed (Table 5). Of these, 46 (35.7%) were carried out in the laboratory, 56 (43.4%) in the field and 27 (20.9%) under natural conditions. Of the laboratory experiments, 7 (15.2%) were conducted in aquaria, 1 (2.2%) in enclosures within tanks, 11 (23.9%) in tanks, 8 (17.4%) in enclosures within artificial ponds, 1 (2.2%) using exclosures within artificial ponds, and 18 (39.1%) in artificial ponds. Of the field experiments, four (7.1%) relied on enclosures within semi-natural ponds, 13 (23.2%) on semi-natural ponds, 20 (35.7%) on enclosures within a water body, 4 (7.1%) on a stocked water body, 14 (25.0%) on exclosures within a water body, and 1 (1.8%) on natural ponds. Finally, the natural experiments were conducted at several spatial scales, ranging from sections of water bodies or river catchments, to individual rivers or lakes, up to entire drainage systems.

There was an exponential increase in the cumulative number of experiments carried out since the 1990s (Figure 2A) in 19 countries across the 5 continents (Table 5). From the 1940s to the 1970s, only laboratory and field experiments were conducted, with no significant differences in proportion amongst decades (Fisher Exact test: $P = 0.790$). Starting from the 1980s, natural experiments were also being conducted and in similar proportion relative to laboratory and field experiments during the four decades until the 2010s ($\chi^2 = 7.08$, d$f = 6$, $P = 0.314$) Figure 2B). Also, of the 102 laboratory and field experiments, 86 (45 laboratory, 41 field) held carp within enclosures and 16 (one laboratory, 15 field) used exclosures.

Evaluation

In total, 373 assessments were made across the reviewed experiments (Table 5), of which 155 (41.6%) in the laboratory, 166 (44.5%) in the field (Table 6), and 52 (13.9%) under natural conditions (Table 7).

Based on component group, there was a significantly higher proportion of natural relative to laboratory- and field-based assessments that quantified the effects of carp on vertebrates, and a significantly lower proportion of natural assessments dealing with invertebrates ($\chi^2 = 24.86$, d$f = 6$, $P < 0.001$); conversely, the proportion of laboratory, field, and natural assessments testing carp effects on water quality and vegetation was overall similar (Figure 3A). Based on experimental plot type, there was a significantly higher proportion of natural (hence, plot-free) assessments evaluating the effects of carp on vertebrates, but a lower proportion of the same evaluating effects on invertebrates ($\chi^2 = 30.81$, d$f = 6$, $P < 0.001$);

Table 5 Reviewed experiments evaluating the effects of carp on freshwater ecosystems, arranged according to experimental location and type of arena (with plot type in parentheses: Ex = exclosures, En = enclosures; see Table 1)

Experiment	Country (risk area)	Size of arena (capacity/area)	Carp: Biomass/density/L/W (age)	Carp: Critical biomass	Conclusions	Abiotic: Water quality: TU	Abiotic: Water quality: N	Abiotic: Water quality: P	Biotic: Vegetation: PH	Biotic: Vegetation: MA	Biotic: Invertebrates: ZP	Biotic: Invertebrates: BI	Biotic: Vertebrates: AM	Biotic: Vertebrates: WF	Biotic: Vertebrates: FI
Laboratory															
Aquaria (En)															
Nuttall and Richardson (1991)	Australia (H)		139.4–150.3 g (0+)		NO		+	+							
Sidorkewicj et al. (1996)	Argentina (M)	0.24 m^2 (100 L)	550–3542 kg ha^{-1} (0+)	550	BK	+				−					
Sidorkewicj et al. (1999a)	Argentina (M)	0.24 m^2 (100 L)	550–3542 kg ha^{-1} (0+)	550	BK	+			+						
Sidorkewicj et al. (1999b) (K, WB)	Argentina (M)	0.24 m^2 (100 L)	550–3542 kg ha^{-1} (0+)	500	BK	+			+	−					
Miller and Provenza (2007)	USA (H)	0.48 m^2 (189 L)	40–65 cm L (0+)		BK					Δ					
Spieth et al. (2011)	Germany (L)	0.25 m^2 (90 L)	100–120 mm TL (0+)		BK							−			
Busst and Britton (2015)	UK (M)	(45 L)	56.3 ± 2.0; 52.2 ± 2.7 (0+)		CA										−
Enclosures within tanks (En)															
Spieth et al. (2011)	Germany (L)	0.49 m^2 (6 m^2)	90–100 mm TL (0+)		BK							−			
Tanks (En)															
Qin and Threlkeld (1990) (K, M)	USA (H)	1.54–4.15 m^2 (900–7000 L)	1.3 ind. m^{-2} (0+)		NO		+	0	+		Δ				
Richardson et al. (1990) (K, M, WB)	USA (H)	4.15 m^2 (7000 L)	18.2 kg ha^{-1} (0+)	18	NO			+	+		Δ	−			
Cline et al. (1994) (K, WB)	USA (H)	1.54 m^2 (900 L)	442 kg ha^{-1} (0+)	442	NO	+	+	0			−	−			
Drenner et al. (1998) (WB)	USA (H)	2.54 m^2 (5500 L)	2209, 2457, 2553, 2760 kg ha^{-1} (0+)	2495	BK-CA	+	+	+	+						
Chumchal and Drenner (2004) (K, M, WB)	USA (H)	2.54 m^2 (5000 L)	670 kg ha^{-1} (0+)	670	NO		+		+		+				
Hinojosa-Garro and Zambrano (2004)* (K, WB)	Mexico (M)	1.77 m^2	12–149 kg ha^{-1}	31	BK-CA							−			
Carey and Wahl (2010)	USA (H)	(1325 L)	4.8 ± 0.64 g (0+)		CA			0	+		Δ	−			−
Hunter et al. (2011)	Australia (H)	(200 L)	60–150 mm TL (0+)		CA								−		
Fischer et al. (2013)	USA (H)	2.54 m^2	4098 kg ha^{-1}	4098	CA	+	+	+	0	−	Δ	−			
Weber and Brown (2013)	USA (H)	4.52 m^2 (4543)	1000 kg ha^{-1}	1000	NO	+	+	+	+	−	+	−			
Weber and Brown (2015)	USA (H)	4.52 m^2 (4543)	175, 475, 812 kg ha^{-1} (0+)	175	NO	+	+	+	+	−	Δ	0			
Enclosures within artificial ponds (En)															
Lamarra (1975) (M)	USA (H)	8.54 m^2 (10 ha)	162–1250 kg ha^{-1}	365	BK			+	+						
Riera et al. (1991) (K)	France (M)	2.5 m^2 (500 m^2)	938 kg ha^{-1}	938	NO							−			
Parkos et al. (2003) (K, M, WB)	USA (H)	546 m^2 (0.4 ha)	174, 476 kg ha^{-1}	174	NO	+		+	+	−	+	−			
Driver et al. (2005) (K, M)	Australia (H)	65 m^2 (0.3 ha)	330, 570, 650 kg ha^{-1}	330	NO	+	+	+	+	−					
Parkos et al. (2006) (WB)	USA (H)	600 m^2 (0.4 ha)	300 kg ha^{-1}	300	SS	+	+	+	0	−	Δ	−			
Wolfe et al. (2009)	USA (H)	546 m^2 (0.4 ha)	319–429 kg ha^{-1}	371	NO	+				−					Δ
Wong et al. (2009)	China (L)	0.8 m^2 (0.1 ha)	148 mm FL		CA					−		−			
Wahl et al. (2011)	USA (H)	600 m^2 (0.4 ha)	276.6–430 kg ha^{-1}	336	NO	+	+	+	−	−	0	−			−

(Continued on next page)

Table 5 Reviewed experiments evaluating the effects of carp on freshwater ecosystems, arranged according to experimental location and type of arena (with plot type in parentheses: Ex = exclosures, En = enclosures; see Table 1) *(Continued)*

Experiment	Country (risk area)	Size of arena (capacity/area)	Carp: Biomass/density/L/W (age)	Carp: Critical biomass	Conclusions	Abiotic: Water quality: TU	Abiotic: Water quality: N	Abiotic: Water quality: P	Biotic: Vegetation: PH	Biotic: Vegetation: MA	Biotic: Invertebrates: ZP	Biotic: Invertebrates: BI	Biotic: Vertebrates: AM	Biotic: Vertebrates: WF	Biotic: Vertebrates: FI
Exclosures within artificial ponds (Ex)															
Zambrano and Hinojosa (1999) (K, WB)	Mexico (M)	2.25 m^2	12–149 kg ha^{-1} (0+)	31	NO-BK					–		–			
Artificial ponds (En)															
Black (1946)	USA (H)	0.74 ha	532 kg ha^{-1}	532	NO					–					
Mraz and Cooper (1957)	USA (H)	0.73–3.56 ha	224 kg ha^{-1}	224	NO	+									–
Olaniyan (1961)	Nigeria (M)		324–648 ind. ha^{-1}		NO	0					0				
Grygierek et al. (1966)	Poland (L)	0.2 ha	2.5–30 kg ha^{-1} (0+)	30	SS				0		+				
Haines (1973) (WB)	USA (H)	51.84 m^2	70 kg ha^{-1}		NO						0	0			0
Forester and Lawrence (1978) (K, WB)	USA (H)	0.1 ha	162 kg ha^{-1}	162	NO	+						–			–
Hume et al. (1983)	Australia (H)	1 ha	80–260 kg ha^{-1}		BK	0				0	0				0
Meijer et al. (1990b) (K, WB)	Netherlands (M)	0.1 ha	396 kg ha^{-1} (0+)	396	NO	+	0	0	+		Δ				
Breukelaar et al. (1994a,b) (K, M)	Netherlands (M)	0.1 ha	179, 330, 525 kg ha^{-1}	330	NO	+									
Tátrai et al. (1994, 1997) (K)	Netherlands (M)	0.1 ha	150, 300, 500 kg ha^{-1}	150	NO	+			+	–	Δ	–			
Roberts et al. (1995) (K, WB)	Australia (H)	12 m^2	226, 510 kg ha^{-1}	510	CA	+	0			–					
Drenner et al. (1997) (K, WB)	USA (H)	0.38 ha	6.8–566.2 kg ha^{-1}	286.5	SS	+				0					–
Drenner et al. (1998) (K, WB)	USA (H)	0.15–0.66 ha	6.8–566.2 kg ha^{-1} (0+)	286.5	BK-CA	+	0	0	+	–	+				0
Swirepik (1999)	Australia (H)		500 kg ha^{-1}	500	NO	+				–					
Zambrano and Hinojosa (1999) (K, WB)	Mexico (M)	500 m^2	12–149 kg ha^{-1} (0+)	31	NO-BK	+				–		0			
Khan et al. (2003) (K, WB)	Australia (H)	5.4 m^2	520 kg ha^{-1}	520	CA	+	0	0	+		–				
Hinojosa-Garro and Zambrano (2004)* (WB)	Mexico (M)	500 m^2	12–149 kg ha^{-1} (0+)	31	BK-CA							–			
Chumchal et al. (2005) (K, WB)	USA (H)	0.36 ha	130–465 kg ha^{-1}	130	NO	0	+	+	+	–	Δ				
Field															
Enclosures within semi-natural ponds (En)															
Matsuzaki et al. (2007) (K, M)	Japan (M)	4 m^2 (0.2925 ha)	369 kg ha^{-1}	369	NO	+	+	–	+	–	+	–			
Matsuzaki et al. (2009a) (WB)	Japan (M)	4 m^2 (0.2925 ha)	161, 323, 484 kg ha^{-1}	161	BK-CA	+	+	–	+	–	+	–			
Kloskowski (2011b)	Poland (L)	1 m^2 (1–69 ha)	330, 600 kg ha^{-1}	330	BK-CA					–		–	–		
Kloskowski (2011c)	Poland (L)	1 m^2 (0.9–23 ha)	203 kg ha^{-1}	203	SS-CA								–		
Semi-natural ponds (En)															
Meijer et al. (1990a) (WB)	Netherlands (M)	1 ha	320 kg ha^{-1}	320	BK	+									
Lewkowicz and Žurek (1991)	Poland (L)	8 ha	20, 190 kg ha^{-1} (0+)	190	NO	+			+						
Denton and Beebee (1997)	UK (M)	19.63 m^2	<10 cm L		CA							–	+		
Tapia and Zambrano (2003) (WB)	Mexico (M)	0.8–8 ha	>2 ind. m^{-2} (0+)		SS-BK	+				–		–	–		
Hinojosa-Garro and Zambrano (2004)* (WB)	Mexico (M)	0.8–8 ha	12–149 kg ha^{-1}	31	BK-CA							–			
Badiou (2005); Badiou and Goldsborough (2010)	USA (H)	5–7 ha	97–1247 kg ha^{-1}	400	BK	+	+	+	+	–					
Haas et al. (2007)	Germany (L)	7 ha	125, 450 kg ha^{-1}	125	SS	+			+	–	–	–		–	
Kloskowski (2009)	Poland (L)	294–682 ha	1000–60,000 ind. ha^{-1}		SS								–		

Kloskowski (2010)	Poland (L)	0.8–23 ha	1000–60,000 ind. ha^{-1}		SS-BK								–	
Kloskowski et al. (2010)	Poland (L)	651–682 ha	225 kg ha^{-1}	225	BK-CA							–	–	Δ
Kloskowski (2011b)	Poland (L)	651–682 ha	170–240 kg ha^{-1}	240	BK-CA	+			+	–				
Kloskowski (2011c)	Poland (L)	0.9–23 ha	51, 203, 243 kg ha^{-1}	203	SS-CA									–
Nieoczym and Kloskowski (2014, 2015)	Poland (L)	1–13 ha	50, 230, 236 kg ha^{-1}	236	CA	+		+	+	0	Δ	–		
Enclosures within a water body (En)														
Robel (1961) (K)	USA (H)	232 m^2	213–701 kg ha^{-1}	213	CA	0				–				
Macrae (1979)	Canada (H)	11 m^2	870, 1640 kg ha^{-1}	1640	NO	0	0	0	0	–		–		
Crivelli (1983) (K, WB)	France (M)	64 m^2	423.8–725.6 kg ha^{-1}	725.6	NO	0				–				
Berry et al. (1990); Kolterman (1990)	USA (H)	115–183 m^2	675 kg ha^{-1}	675	NO	0				–				
Wilcox and Hornbach (1991) (K, WB)	USA (H)	15 m^2	153, 460, 1128 kg ha^{-1}	153	NO							–		
Batzer (1998) (M)	USA (H)	2.25 m^2	17.8 ind. m^{-2} (0+)		CA							–		
Lougheed et al. (1998) (K, WB)	Canada (H)	50 m^2	22.8–2093 kg ha^{-1}	500	BK-CA	+	+	Δ	0		0			
Chow-Fraser (1999)	Canada (H)	50 m^2	1000 ind. ha^{-1}		BK	+								
Angeler et al. (2002a) (K, WB)	Spain (M)	0.78 m^2	7051, 7372, 8333 kg ha^{-1}	7051	CA	+	+	+	+		–			
Angeler et al. (2002b)[§]	Spain (M)	0.78 m^2	7051, 7372, 8333 kg ha^{-1}	7051	NO	+	+	+	+		+			
Williams et al. (2002); Williams and Moss (2002) (K, M, WB)	UK (M)	4 m^2	200, 700, 800 kg ha^{-1}	800	NO	+	0	+	+	–	Δ	–		
Angeler and Rodrigo (2004)[†]	Spain (M)	0.78 m^2	7051, 7372, 8333 kg ha^{-1}	7051	CA	+	+		+		0			
Badiou (2005)	USA (M)	25 m^2	600–1540 kg ha^{-1}	600	BK	+	+	+	+	–	+	–		
Miller and Crowl (2006) (M, WB)	USA (M)	6.25 m^2	163 kg ha^{-1}	163	BK					–		–		
Angeler et al. (2007)[**]	Spain (M)	0.78 m^2	7051, 7372, 8333 kg ha^{-1}	7051	NO	+	+				–			
Roozen et al. (2007) (K, WB)	Netherlands (M)	0.87 m^2	2931 kg ha^{-1}	2931	BK-CA		+	+	+		0			
Özbay (2008)	Turkey (L)	6.25 m^2	1000 kg ha^{-1}	1000	NO	+	0	0	+	–	0			
Akhurst et al. (2012)	Australia (H)	3.14 m^2	1875 kg ha^{-1}	1875	CA	+	+	+	+	–	0			
Wells (2013)	USA (H)	2.25 m^2	19,375–24,757 kg ha^{-1}	19,375	NO	+								
Ip et al. (2014)	China (L)	1 m^2	170–195 mm FL		SS					–		–		
Stocked water body (En)														
Guziur and Wielgosz (1975)	Poland (L)	29.3 ha	13, 43 kg ha^{-1} (0+)	43	SS							–		
King et al. (1997); Robertson et al. (1997) (K, WB)	Australia (H)	0.280; 0.851 ha	101, 348, 669, 1181 kg ha^{-1}	764.5	SS	+			+					
Sidorkewicj et al. (1998) (K, M, WB)	Argentina (M)	150–200 m^2	18–535 kg ha^{-1}	210	SS-BK	+				–				
Barthelmes and Brämick (2003)	Germany (L)	10.2 ha	200–500 kg ha^{-1}	200	SS							–		0
Exclosures within a water body (Ex)														
Threinen and Helm (1954) (WB)	USA (H)	18.68 m^2			BK					–				
Tryon (1954) (K)	USA (H)	40.47 m^2			CA	0				–				
King and Hunt (1967) (K, WB)	USA (H)	4.55 m^2			BK					–				
ten Winkel and Meulemans (1984)	Netherlands (M)	4 m^2			BK					–				
Harris and Gutzmer (1996)	USA (H)	6 m^2			NO	+				–				
Sager et al. (1998)	Canada (H)	4 m^2			NO	+			+	–				
Batzer et al. (2000)[§§]	USA (H)	2.25 m^2			NO							Δ		
Bartsch et al. (2005)	USA (H)	0.19 m^2			NO							–		
Bowers et al. (2005)	USA (H)	0.56–1 m^2			CA							–		
Sandsten et al. (2005)	Turkey (L)	4 m^2			NO					0		0		
Evelsizer and Turner (2006) (K, M, WB)	USA (H)	9 m^2			NO					–				
Miller and Crowl (2006) (K, WB)	USA (H)	75 m^2			BK				0	–	0	0		

(Continued on next page)

Table 5 Reviewed experiments evaluating the effects of carp on freshwater ecosystems, arranged according to experimental location and type of arena (with plot type in parentheses: Ex = exclosures, En = enclosures; see Table 1) *(Continued)*

			Carp			Abiotic			Biotic						
						Water quality			Vegetation		Invertebrates		Vertebrates		
Experiment	Country (risk area)	Size of arena (capacity/area)	Biomass/density/L/W (age)	Critical biomass	Conclusions	TU	N	P	PH	MA	ZP	BI	AM	WF	FI
Bowers and de Szalay (2007)	USA (H)	1 m^2			CA							–			
Vilizzi et al. (2014b)	Australia (H)	400 m^2	68 kg ha^{-1}	68	CA	+				–	Δ	–			
Natural ponds (Ex)															
Hnatiuk (2006); Parks (2006); Hertam (2010)	Canada (H)	0.83–11.85 ha			SS	+	+	+	+	–		–	–		–
Natural															
Hume et al. (1983); Fletcher et al. (1985) (K)	Australia (H)	80–7760 ha	150, 180, 690 kg ha^{-1}	690		0				Δ					
Swar and Gurung (1988)	Nepal (M)	225 ha	92 kg ha^{-1}	92											–
Bowmer et al. (1994)	Australia (H)		430, 469 kg ha^{-1}	430		+	+	+							
Meredith et al. (1995)	Australia (H)							0							
Miller and Beckman (1996)	USA (H)														–
Fernández et al. (1998) (K)	Argentina (M)		130 kg ha^{-1}	130		+				–					
Lougheed et al. (1998) (WB)	Canada (H)	250 ha	400–3500 ind. ha^{-1}			+				–					
Specziár et al. (1998)	Hungary (N)	59,300 ha													–
Chow-Fraser (1999)	Canada (H)	250 ha				+									
Zambrano et al. (1999) (K, WB)	Mexico (M)	1–8 ha				+	0	0	0	–	0	–			0
Barton et al. (2000) (K, WB)	Canada (H)	0.6 ha	490 kg ha^{-1}	490		+									
Beklioğlu et al. (2000)	Turkey (L)	125 ha	160 kg ha^{-1}	160		+	+	+	+		–				
Egertson and Downing (2004) (WB)	USA (H)	6–743 ha													Δ
Titus et al. (2004)	USA (H)	12 ha								–					
Beklioglu et al. (2006)	Turkey (L)	6800–24,000 ha								–					
Britton et al. (2007) (K)	Kenya (M)	15,000 ha								+					
Rowe (2007)	New Zealand (H)	5–3440 ha				+									
Cardona et al. (2008) (K)	Spain (M)	–													–
Stewart and Downing (2008) (WB)	USA (H)	0.15–1.99 ha	11,036–15,331 ind. m^{-3}			+						–			
Bajer et al. (2009)	USA (H)	508 ha	10–255 kg ha^{-1}	100						–				–	
Jackson et al. (2010)	USA (H)	4–2174 ha	1.6 kg per net night			+	+	+							–
Zambrano et al. (2010)	Mexico (M)	–											–		
Weber and Brown (2011)	USA (H)	16–6289 ha	4.7 trap-net CPUE[††]			+	+	+	+						–
Caithamer (2012)	USA (H)	133, 541 ha												–	
Mazumder et al. (2012)	Australia (H)	3.2–72.7 ha													–
Andreu-Soler and Ruiz-Campos (2013)	Mexico (M)	–	46.2–72.3% BPUE[***]												–
La Porte et al. (2014)	USA (H)	18,500 ha												–	

[*]Biomass range from Zambrano and Hinojosa (1999).
[§]Bacterioplankton and autotrophic picoplankton.
[†]Picoplankton.
**Seston.
[§§]Epiphytic midges.
CPUE = catch per unit effort; BPUE = biomass per unit effort. For each experiment, indication is provided of source study, previous review(s) (K = Kulhanek et al., 2011; M = Matsuzaki et al., 2009a; WB = Weber and Brown 2009), and country (risk area in parentheses: N = no, L = low, M = moderate, H = high; see Table 8). Size of arena: area (m^2 or ha, if ≥ 1000 m^2) as provided in source study or estimated (e.g., from diameter of tanks) with indication of capacity of aquari/atanks or area of containing tanks/ponds (in parentheses). Carp biomass (single value, multiple values, or range, as originally provided), else length (mean or min–max range: L = unspecified length; FL = fork length; TL = total length), weight (mean ± SE) or density (ind. = individuals) of stocked fish, or other measures, with indication of 0+ fish in parentheses. Critical biomass values for carp having an effect in kg ha^{-1}. Conclusions for field/laboratory experiments as per Table 3. Freshwater ecosystem components: TU = turbidity/suspended solids; N = nitrogen; P = Phosphorus; PH = phytoplankton/chlorophyll *a*; MA = aquatic macrophytes; ZP = zooplankton; BI = benthic invertebrates; AM = amphibians; WF = waterfowl; FI = fish. For each assessment (i.e., experiment evaluating the effects of carp on a certain component) notation as per Table 2.

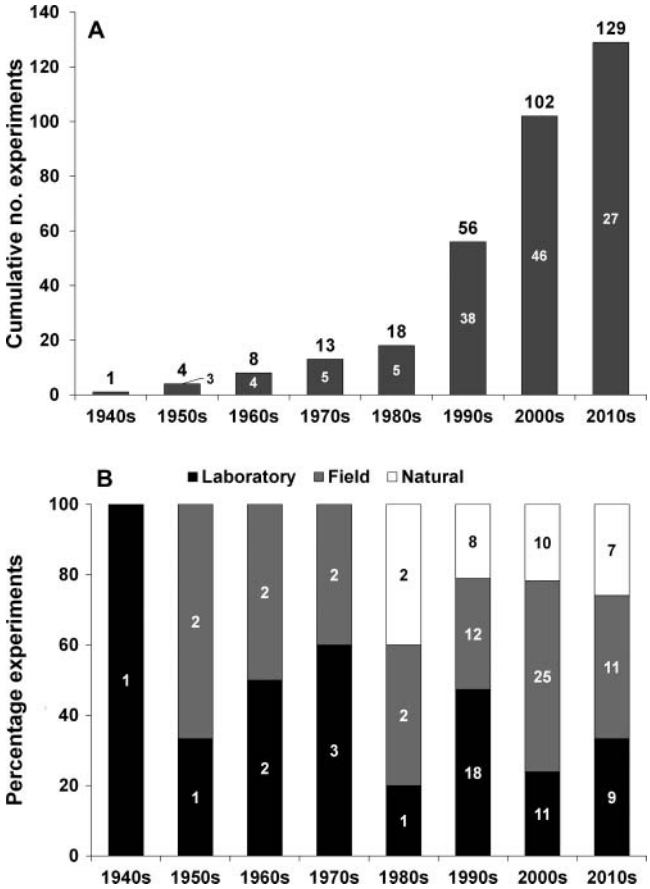

Figure 2 (A) Cumulative number of experiments evaluating carp effects on freshwater ecosystems carried out over the last eight decades (absolute numbers also indicated). (B) Proportion of laboratory, field, and natural experiments (with sub-totals) over the study period.

whereas, the proportion of assessments using enclosures, exclosures or plot-free evaluating effects of carp on water quality and vegetation was overall similar, with the possible exception of a slightly lower proportion of exclosure-based assessments on water quality (Figure 3B).

According to fish age, there was a significantly higher proportion of laboratory than field studies and (especially) natural assessments that evaluated the ecological effects of 0+ carp, and of natural experiments evaluating those of 1+ and older individuals ($\chi^2 = 86.82$, d$f = 2$, $P < 0.001$), with no experiments on the latter under natural conditions (Figure 3C). Similarly, there was a proportionally higher ($\chi^2 = 22.38$, d$f = 2$, $P < 0.001$) number of assessments with 0+ carp being held in enclosures than "free-ranging" based on exclosure or natural experiments (Figure 3D).

There were no statistically significant differences in mean evidence weight from laboratory- and field-based assessments amongst component groups (PERANOVA: $F^{\#}_{3,311} = 0.44$, $P_{\text{permutational}} = 0.718$), nor were any significant differences between/individual components within each group ($F^{\#}_{6,311} = 1.32$, $P_{\text{permutational}} = 0.242$). However, regardless of statistical significance, the mean evidence weight of assessments dealing with carp effects on fish was higher relative to all other components (Figure 4A).

A considerably higher proportion of assessments (66–87%) found carp to increase turbidity/suspended solids, nitrogen, phosphorus, and phytoplankton/chlorophyll *a*, even though 13–29% of these assessments did not detect any effect, and an even smaller proportion (2–5%) found a decrease, or just non-directional change (2%) (Figure 4B). Conversely, carp was generally found (68–90% of assessments) to cause a decrease in the abundance of aquatic macrophytes, benthic invertebrates, amphibians, waterfowl, and fish, even though no change was detected for fish (32% of assessments), benthic invertebrates (10%), and aquatic macrophytes (7%). Whereas, a non-directional change was found in 17% of assessments on waterfowl, 9% on fish, and 3% on macrophytes, with an increase by 10% of the assessments on amphibians and 2% on macrophytes. Finally, the proportion of assessments on zooplankton was equally balanced between change and no effect, with lower proportions for increase and decrease.

Of the 19 countries for which studies were reviewed, only 1 (in Hungary) was categorized as "no risk," with a score of 0 (Table 8). "Low-risk" areas (scores of 2–4) included Central European countries (Poland, Germany), south-east Asia (China), and the Mediterranean region (Turkey). Areas attracting "medium risk" scores (5–8) included Western Europe (France, Netherlands, United Kingdom, and Spain), Central Asia (Nepal), and the Far East (Japan), Africa (Nigeria) as well as both North (Mexico) and Southern America (Argentina). Areas attracting a "high risk" score (10 or 11) were North America (Canada, USA) and Australasia (Australia), all receiving the maximum score, whereas New Zealand received a score of 10.

The relative number of experiments carried out in high-risk areas was considerably higher than in other areas, and there were a higher number of experiments from low-risk than medium-risk areas (Figure 5A). Conversely, there were no significant differences ($\chi^2 = 2.27$, d$f = 6$, $P = 0.893$) in the relative proportion of assessments on the four component groups carried out in low-, medium-, and high-risk areas, with a larger proportion of assessments from the latter across all groups (Figure 5B).

Cause–effect Relationships

The extent of experimental evidence provided in support to each of the 10 hypotheses (i.e., for a carp impact on the corresponding components) differed depending on location of the experiment (Table 9; see also Tables 6 and 7). Thus, laboratory experiments provided support only for the hypothesis of a decrease in benthic invertebrates. Whereas, inconsistent evidence was available for impacts on turbidity/suspended solids, nitrogen, phosphorus, Phytoplankton/chlorophyll *a*, aquatic macrophytes, zooplankton, and fish, with insufficient evidence available for impacts on

Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1)

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Turbidity/suspended solids	(Increase)						
Laboratory							
Sidorkewicj et al. (1996)	Increase	Yes	3	0	1	1	1
Sidorkewicj et al. (1999a)	Increase	Yes	3	0	1	1	1
Sidorkewicj et al. (1999b)	Increase	Yes	3	0	1	1	1
Cline et al. (1994)	Increase	Yes	4	2	1	1	0
Drenner et al. (1998)	Increase	Yes	5	2	1	1	1
Fischer et al. (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2015)	Increase	Yes	4	2	1	1	0
Parkos et al. (2003)	Increase	Yes	5	3	1	1	0
Driver et al. (2005)	Increase	Yes	5	3	1	1	0
Parkos et al. (2006)	Increase	Yes	7	3	1	1	2
Wolfe et al. (2009)	Increase	Yes	5	3	1	1	0
Wahl et al. (2011)	Increase	Yes	5	3	1	1	0
Mraz and Cooper (1957)	Increase	Yes	6	5	0	1	0
Olaniyan (1961)	None	No	6	5	0	1	0
Forester and Lawrence (1978)	Increase	Yes	7	5	1	1	0
Hume et al. (1983)	None	No	8	5	1	1	1
Meijer et al. (1990a)	Increase	Yes	7	5	1	1	0
Breukelaar et al. (1994a,b)	Increase	Yes	7	5	1	1	0
Tátrai et al. (1994, 1997)	Increase	Yes	7	5	1	1	0
Roberts et al. (1995)	Increase	Yes	7	5	1	1	0
Drenner et al. (1997)	Increase	Yes	9	5	1	1	2
Drenner et al. (1998)	Increase	Yes	8	5	1	1	1
Swirepik (1999)	Increase	Yes	7	5	1	1	0
Zambrano and Hinojosa (1999)	Increase	Yes	7	5	0	1	1
Khan et al. (2003)	Increase	Yes	7	5	1	1	0
Chumchal et al. (2005)	None	No	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Increase	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Increase	Yes	3	0	1	1	1
Meijer et al. (1990b)	Increase	Yes	3	1	0	1	1
Lewkowicz and Žurek (1991)	Increase	Yes	2	1	0	1	0
Tapia and Zambrano (2003)	Increase	Yes	4	1	0	1	2
Badiou (2005); Badiou and Goldsborough (2010)	Increase	Yes	4	1	1	1	1
Haas et al. (2007)	Increase	Yes	5	1	1	1	2
Kloskowski (2011b)	Increase	Yes	4	1	1	1	1
Nieoczym and Kloskowski (2014, 2015)	Increase	Yes	3	1	1	1	0
Robel (1961)	None	No	4	2	1	1	0
Macrae (1979)	None	No	4	2	1	1	0
Crivelli (1983)	None	No	4	2	1	1	0
Berry et al. (1990); Kolterman (1990)	None	No	4	2	1	1	0
Lougheed et al. (1998)	Increase	Yes	5	2	1	1	1
Chow-Fraser (1999)	Increase	Yes	5	2	1	1	1
Angeler et al. (2002a)	Increase	Yes	4	2	1	1	0
Angeler et al. (2002b)	Increase	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Increase	Yes	4	2	1	1	0
Angeler and Rodrigo (2004)	Increase	Yes	4	2	1	1	0
Badiou (2005)	Increase	Yes	5	2	1	1	1
Angeler et al. (2007)	Increase	Yes	4	2	1	1	0
Özbay (2008)	Increase	Yes	4	2	1	1	0
Akhurst et al. (2012)	Increase	Yes	4	2	1	1	0
Wells (2013)	Increase	Yes	3	2	1	0	0
King et al. (1997); Robertson et al. (1997)	Increase	Yes	7	3	1	1	2
Sidorkewicj et al. (1998)	Increase	Yes	8	3	1	1	3

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

			Weight				
Citation	Effect	Support	Total	Setup	Replication	Control	Conclusions
Tryon (1954)	None	No	6	4	1	1	0
Harris and Gutzmer (1996)	Increase	Yes	5	4	1	0	0
Sager et al. (1998)	Increase	Yes	6	4	1	1	0
Vilizzi et al. (2014b)	Increase	Yes	6	4	1	1	0
Hnatiuk (2006); Parks (2006); Hertam (2010)	Increase	Yes	9	5	1	1	2
Nitrogen	(Increase)						
Laboratory							
Nuttall and Richardson (1991)	Increase	Yes	1	0	0	1	0
Qin and Threlkeld (1990)	Increase	Yes	4	2	1	1	0
Cline et al. (1994)	Increase	Yes	4	2	1	1	0
Drenner et al. (1998)	Increase	Yes	5	2	1	1	1
Chumchal and Drenner (2004)	Increase	Yes	4	2	1	1	0
Fischer et al. (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2015)	Increase	Yes	4	2	1	1	0
Driver et al. (2005)	Increase	Yes	5	3	1	1	0
Parkos et al. (2006)	Increase	Yes	7	3	1	1	2
Wahl et al. (2011)	Increase	Yes	5	3	1	1	0
Meijer et al. (1990a)	None	No	7	5	1	1	0
Roberts et al. (1995)	None	No	7	5	1	1	0
Drenner et al. (1998)	None	No	8	5	1	1	1
Khan et al. (2003)	None	No	7	5	1	1	0
Chumchal et al. (2005)	Increase	Yes	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Increase	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Increase	Yes	3	0	1	1	1
Badiou (2005); Badiou and Goldsborough (2010)	Increase	Yes	4	1	1	1	1
Macrae (1979)	None	No	4	2	1	1	0
Lougheed et al. (1998)	Increase	Yes	5	2	1	1	1
Angeler et al. (2002a)	Increase	Yes	4	2	1	1	0
Angeler et al. (2002b)	Increase	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	None	No	4	2	1	1	0
Angeler and Rodrigo (2004)	Increase	Yes	4	2	1	1	0
Badiou (2005)	Increase	Yes	5	2	1	1	1
Angeler et al. (2007)	Increase	Yes	4	2	1	1	0
Roozen et al. (2007)	Increase	Yes	5	2	1	1	1
Özbay (2008)	None	No	4	2	1	1	0
Akhurst et al. (2012)	Increase	Yes	4	2	1	1	0
Hnatiuk (2006); Parks (2006); Hertam (2010)	Increase	Yes	9	5	1	1	2
Phosphorus	(Increase)						
Laboratory							
Nuttall and Richardson (1991)	Increase	Yes	1	0	0	1	0
Qin and Threlkeld (1990)	None	No	4	2	1	1	0
Richardson et al. (1990)	Increase	Yes	4	2	1	1	0
Cline et al. (1994)	None	No	4	2	1	1	0
Drenner et al. (1998)	Increase	Yes	5	2	1	1	1
Carey and Wahl (2010)	None	No	4	2	1	1	0
Fischer et al. (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2015)	Increase	Yes	4	2	1	1	0
Lamarra (1975)	Increase	Yes	6	3	1	1	1
Parkos et al. (2003)	Increase	Yes	5	3	1	1	0
Driver et al. (2005)	Increase	Yes	5	3	1	1	0
Parkos et al. (2006)	Increase	Yes	7	3	1	1	2
Wahl et al. (2011)	Increase	Yes	5	3	1	1	0
Meijer et al. (1990a)	None	No	7	5	1	1	0

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Drenner et al. (1998)	None	No	8	5	1	1	1
Khan et al. (2003)	None	No	7	5	1	1	0
Chumchal et al. (2005)	Increase	Yes	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Decrease	No	2	0	1	1	0
Matsuzaki et al. (2009)	Decrease	No	3	0	1	1	1
Badiou (2005); Badiou and Goldsborough (2010)	Increase	Yes	4	1	1	1	1
Nieoczym and Kloskowski (2014, 2015)	Increase	Yes	3	1	1	1	0
Macrae (1979)	None	No	4	2	1	1	0
Lougheed et al. (1998)	Change	No	5	2	1	1	1
Angeler et al. (2002a)	Increase	Yes	4	2	1	1	0
Angeler et al. (2002b)	Increase	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Increase	Yes	4	2	1	1	0
Badiou (2005)	Increase	Yes	5	2	1	1	1
Roozen et al. (2007)	Increase	Yes	5	2	1	1	1
Özbay (2008)	None	No	4	2	1	1	0
Akhurst et al. (2012)	Increase	Yes	4	2	1	1	0
Hnatiuk (2006); Parks (2006); Hertam (2010)	Increase	Yes	9	5	1	1	2
Phytoplankton/chlorophyll *a*	(Increase)						
Laboratory							
Sidorkewicj et al. (1999a)	Increase	Yes	3	0	1	1	1
Sidorkewicj et al. (1999b)	Increase	Yes	3	0	1	1	1
Qin and Threlkeld (1990)	Increase	Yes	4	2	1	1	0
Richardson et al. (1990)	Increase	Yes	4	2	1	1	0
Drenner et al. (1998)	Increase	Yes	5	2	1	1	1
Chumchal and Drenner (2004)	Increase	Yes	4	2	1	1	0
Carey and Wahl (2010)	Increase	Yes	4	2	1	1	0
Fischer et al. (2013)	None	No	4	2	1	1	0
Weber and Brown (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2015)	Increase	Yes	4	2	1	1	0
Lamarra (1975)	Increase	Yes	6	3	1	1	1
Parkos et al. (2003)	Increase	Yes	5	3	1	1	0
Driver et al. (2005)	Increase	Yes	5	3	1	1	0
Parkos et al. (2006)	None	No	7	3	1	1	2
Wahl et al. (2011)	Decrease	No	5	3	1	1	0
Grygierek et al. (1966)	None	No	9	5	1	1	2
Meijer et al. (1990a)	Increase	Yes	7	5	1	1	0
Tátrai et al. (1994, 1997)	Increase	Yes	7	5	1	1	0
Drenner et al. (1998)	Increase	Yes	8	5	1	1	1
Khan et al. (2003)	None	No	7	5	1	1	0
Chumchal et al. (2005)	Increase	Yes	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Increase	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Increase	Yes	3	0	1	1	1
Lewkowicz and Žurek (1991)	Increase	Yes	2	1	0	1	0
Badiou (2005); Badiou and Goldsborough (2010)	Increase	Yes	4	1	1	1	1
Haas et al. (2007)	Increase	Yes	5	1	1	1	2
Kloskowski (2011b)	Increase	Yes	4	1	1	1	1
Nieoczym and Kloskowski (2014, 2015)	Increase	Yes	3	1	1	1	0
Macrae (1979)	None	No	4	2	1	1	0
Lougheed et al. (1998)	None	No	5	2	1	1	1
Angeler et al. (2002a)	Increase	Yes	4	2	1	1	0
Angeler et al. (2002b)	Increase	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Increase	Yes	4	2	1	1	0
Angeler and Rodrigo (2004)	Increase	Yes	4	2	1	1	0
Badiou (2005)	Increase	Yes	5	2	1	1	1

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Roozen et al. (2007)	Increase	Yes	5	2	1	1	1
Özbay (2008)	Increase	Yes	4	2	1	1	0
Akhurst et al. (2012)	Increase	Yes	4	2	1	1	0
King et al. (1997); Robertson et al. (1997)	Increase	Yes	7	3	1	1	2
Sager et al. (1998)	Increase	Yes	6	4	1	1	0
Miller and Crowl (2006)	None	No	7	4	1	1	1
Hnatiuk (2006); Parks (2006); Hertam (2010)	Increase	Yes	9	5	1	1	2
Aquatic macrophytes	(Decrease)						
Laboratory							
Sidorkewicj et al. (1996)	Decrease	Yes	3	0	1	1	1
Sidorkewicj et al. (1999b)	Decrease	Yes	3	0	1	1	1
Miller and Provenza (2007)	Change	No	3	0	1	1	1
Fischer et al. (2013)	Decrease	Yes	4	2	1	1	0
Weber and Brown (2013)	Decrease	Yes	4	2	1	1	0
Weber and Brown (2015)	Decrease	Yes	4	2	1	1	0
Parkos et al. (2003)	Decrease	Yes	5	3	1	1	0
Driver et al. (2005)	Decrease	Yes	5	3	1	1	0
Parkos et al. (2006)	Decrease	Yes	7	3	1	1	2
Wolfe et al. (2009)	Decrease	Yes	5	3	1	1	0
Wong et al. (2009)	Decrease	Yes	5	3	1	1	0
Wahl et al. (2011)	Decrease	Yes	5	3	1	1	0
Zambrano and Hinojosa (1999)	Decrease	Yes	7	4	1	1	1
Black (1946)	Decrease	Yes	6	5	0	1	0
Hume et al. (1983)	None	No	8	5	1	1	1
Tátrai et al. (1994, 1997)	Decrease	Yes	7	5	1	1	0
Roberts et al. (1995)	Decrease	Yes	7	5	1	1	0
Drenner et al. (1997)	None	No	9	5	1	1	2
Drenner et al. (1998)	Decrease	Yes	8	5	1	1	1
Swirepik (1999)	Decrease	Yes	7	5	1	1	0
Zambrano and Hinojosa (1999)	Decrease	Yes	7	5	0	1	1
Chumchal et al. (2005)	Decrease	Yes	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Decrease	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Decrease	Yes	3	0	1	1	1
Kloskowski (2011b)	Decrease	Yes	3	0	1	1	1
Tapia and Zambrano (2003)	Decrease	Yes	4	1	0	1	2
Badiou (2005); Badiou and Goldsborough (2010)	Decrease	Yes	4	1	1	1	1
Haas et al. (2007)	Decrease	Yes	5	1	1	1	2
Kloskowski (2011b)	Decrease	Yes	4	1	1	1	1
Nieoczym and Kloskowski (2014, 2015)	None	No	3	1	1	1	0
Robel (1961)	Decrease	Yes	4	2	1	1	0
Macrae (1979)	Decrease	Yes	4	2	1	1	0
Crivelli (1983)	Decrease	Yes	4	2	1	1	0
Berry et al. (1990); Kolterman (1990)	Decrease	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Decrease	Yes	4	2	1	1	0
Badiou (2005)	Decrease	Yes	5	2	1	1	1
Miller and Crowl (2006)	Decrease	Yes	5	2	1	1	1
Özbay (2008)	Decrease	Yes	4	2	1	1	0
Akhurst et al. (2012)	Decrease	Yes	4	2	1	1	0
Ip et al. (2014)	Decrease	Yes	6	2	1	1	2
Sidorkewicj et al. (1998)	Decrease	Yes	8	3	1	1	3
Threinen and Helm (1954)	Decrease	Yes	6	4	1	0	1
Tryon (1954)	Decrease	Yes	6	4	1	1	0
King and Hunt (1967)	Decrease	Yes	6	4	1	0	1
ten Winkel and Meulemans (1984)	Decrease	Yes	6	4	1	0	1
Harris and Gutzmer (1996)	Decrease	Yes	5	4	1	0	0

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Sager et al. (1998)	Decrease	Yes	6	4	1	1	0
Sandsten et al. (2005)	None	No	6	4	1	1	0
Evelsizer and Turner (2006)	Decrease	Yes	6	4	1	1	0
Miller and Crowl (2006)	Decrease	Yes	7	4	1	1	1
Vilizzi et al. (2014b)	Decrease	Yes	6	4	1	1	0
Hnatiuk (2006); Parks (2006); Hertam (2010)	Decrease	Yes	9	5	1	1	2
Zooplankton	(Change)						
Laboratory							
Qin and Threlkeld (1990)	Change	Yes	4	2	1	1	0
Richardson et al. (1990)	Change	Yes	4	2	1	1	0
Cline et al. (1994)	Decrease	Yes	4	2	1	1	0
Chumchal and Drenner (2004)	Increase	Yes	4	2	1	1	0
Carey and Wahl (2010)	Change	Yes	4	2	1	1	0
Fischer et al. (2013)	Change	Yes	4	2	1	1	0
Weber and Brown (2013)	Increase	Yes	4	2	1	1	0
Weber and Brown (2015)	Change	Yes	4	2	1	1	0
Parkos et al. (2003)	Increase	Yes	5	3	1	1	0
Parkos et al. (2006)	Change	Yes	7	3	1	1	2
Wahl et al. (2011)	None	No	5	3	1	1	0
Olaniyan (1961)	None	No	6	5	0	1	0
Grygierek et al. (1966)	Increase	Yes	9	5	1	1	2
Haines (1973)	None	No	7	5	1	1	0
Hume et al. (1983)	None	No	8	5	1	1	1
Meijer et al. (1990a)	Change	Yes	7	5	1	1	0
Tátrai et al. (1994, 1997)	Change	Yes	7	5	1	1	0
Drenner et al. (1998)	Increase	Yes	8	5	1	1	1
Khan et al. (2003)	Decrease	Yes	7	5	1	1	0
Chumchal et al. (2005)	Change	Yes	7	5	1	1	0
Field							
Matsuzaki et al. (2007)	Increase	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Increase	Yes	3	0	1	1	1
Haas et al. (2007)	Decrease	Yes	5	1	1	1	2
Nieoczym and Kloskowski (2014, 2015)	Change	Yes	3	1	1	1	0
Lougheed et al. (1998)	None	No	5	2	1	1	1
Angeler et al. (2002a)	Decrease	Yes	4	2	1	1	0
Angeler et al. (2002b)	Increase	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Change	Yes	4	2	1	1	0
Angeler and Rodrigo (2004)	None	No	4	2	1	1	0
Badiou (2005)	Increase	Yes	5	2	1	1	1
Angeler et al. (2007)	Decrease	Yes	4	2	1	1	0
Roozen et al. (2007)	None	No	5	2	1	1	1
Özbay (2008)	None	No	4	2	1	1	0
Akhurst et al. (2012)	None	No	4	2	1	1	0
Miller and Crowl (2006)	None	No	7	4	1	1	1
Vilizzi et al. (2014b)	Change	Yes	6	4	1	1	0
Benthic invertebrates	(Decrease)						
Laboratory							
Spieth et al. (2011)	Decrease	Yes	3	0	1	1	1
Spieth et al. (2011)	Decrease	Yes	4	1	1	1	1
Richardson et al. (1990)	Decrease	Yes	4	2	1	1	0
Cline et al. (1994)	Decrease	Yes	4	2	1	1	0
Hinojosa-Garro and Zambrano (2004)	Decrease	Yes	4	2	0	1	1
Carey and Wahl (2010)	Decrease	Yes	4	2	1	1	0
Fischer et al. (2013)	Decrease	Yes	4	2	1	1	0
Weber and Brown (2013)	Decrease	Yes	4	2	1	1	0
Weber and Brown (2015)	None	No	4	2	1	1	0

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Riera et al. (1991)	Decrease	Yes	4	3	1	0	0
Parkos et al. (2003)	Decrease	Yes	5	3	1	1	0
Parkos et al. (2006)	Decrease	Yes	7	3	1	1	2
Wong et al. (2009)	Decrease	Yes	5	3	1	1	0
Wahl et al. (2011)	Decrease	Yes	5	3	1	1	0
Zambrano and Hinojosa (1999)	Decrease	Yes	7	4	1	1	1
Haines (1973)	None	No	7	5	1	1	0
Forester and Lawrence (1978)	Decrease	Yes	7	5	1	1	0
Tátrai et al. (1994, 1997)	Decrease	Yes	7	5	1	1	0
Zambrano and Hinojosa (1999)	None	No	7	5	0	1	1
Hinojosa-Garro and Zambrano (2004)	Decrease	Yes	7	5	0	1	1
Field							
Matsuzaki et al. (2007)	Decrease	Yes	2	0	1	1	0
Matsuzaki et al. (2009)	Decrease	Yes	3	0	1	1	1
Kloskowski (2011b)	Decrease	Yes	3	0	1	1	1
Denton and Beebee (1997)	Decrease	Yes	3	1	1	1	0
Tapia and Zambrano (2003)	Decrease	Yes	4	1	0	1	2
Hinojosa-Garro and Zambrano (2004)	Decrease	Yes	3	1	0	1	1
Haas et al. (2007)	Decrease	Yes	5	1	1	1	2
Kloskowski et al. (2010)	Decrease	Yes	4	1	1	1	1
Nieoczym and Kloskowski (2014, 2015)	Decrease	Yes	3	1	1	1	0
Macrae (1979)	Decrease	Yes	4	2	1	1	0
Wilcox and Hornbach (1991)	Decrease	Yes	4	2	1	1	0
Batzer (1998)	Decrease	Yes	4	2	1	1	0
Williams et al. (2002); Williams and Moss (2003)	Decrease	Yes	4	2	1	1	0
Badiou (2005)	Decrease	Yes	5	2	1	1	1
Miller and Crowl (2006)	Decrease	Yes	5	2	1	1	1
Ip et al. (2014)	Decrease	Yes	6	2	1	1	2
Guziur and Wielgosz (1975)	Decrease	Yes	5	3	0	0	2
Barthelmes and Brämick (2003)	Decrease	Yes	5	3	0	0	2
Batzer et al. (2000)	Change	No	6	4	1	1	0
Bartsch et al. (2005)	Decrease	Yes	6	4	1	1	0
Bowers et al. (2005)	Decrease	Yes	6	4	1	1	0
Sandsten et al. (2005)	None	No	6	4	1	1	0
Miller and Crowl (2006)	None	No	7	4	1	1	1
Bowers and de Szalay (2007)	Decrease	Yes	6	4	1	1	0
Vilizzi et al. (2014b)	Decrease	Yes	6	4	1	1	0
Hnatiuk (2006); Parks (2006); Hertam (2010)	Decrease	Yes	9	5	1	1	2
Amphibians	(Decrease)						
Laboratory							
Hunter et al. (2011)	Decrease	Yes	4	2	1	1	0
Field							
Kloskowski (2011b)	Decrease	Yes	3	0	1	1	1
Kloskowski (2011c)	Decrease	Yes	4	0	1	1	2
Denton and Beebee (1997)	Increase	No	3	1	1	1	0
Tapia and Zambrano (2003)	Decrease	Yes	4	1	0	1	2
Kloskowski (2009)	Decrease	Yes	5	1	1	1	2
Kloskowski (2010)	Decrease	Yes	6	1	1	1	3
Kloskowski et al. (2010)	Decrease	Yes	4	1	1	1	1
Hnatiuk (2006); Parks (2006); Hertam (2010)	Decrease	Yes	9	5	1	1	2
Waterfowl	(Decrease)						
Field							
Haas et al. (2007)	Decrease	Yes	5	1	1	1	2
Kloskowski et al. (2010)	Change	No	4	1	1	1	1
Kloskowski (2011c)	Decrease	Yes	5	1	1	1	2

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Table 6 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for laboratory and field experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight				
			Total	Setup	Replication	Control	Conclusions
Fish	(Decrease)						
Laboratory							
Busst and Britton (2015)	Decrease	Yes	2	0	1	1	0
Carey and Wahl (2010)	Decrease	Yes	4	2	1	1	0
Wolfe et al. (2009)	Change	No	5	3	1	1	0
Wahl et al. (2011)	Decrease	Yes	5	3	1	1	0
Mraz and Cooper (1957)	Decrease	Yes	6	5	0	1	0
Haines (1973)	None	No	7	5	1	1	0
Forester and Lawrence (1978)	Decrease	Yes	7	5	1	1	0
Hume et al. (1983)	None	No	8	5	1	1	1
Drenner et al. (1997)	Decrease	Yes	9	5	1	1	2
Drenner et al. (1998)	None	No	8	5	1	1	1
Field							
Barthelmes and Brämick (2003)	None	No	5	3	0	0	2
Hnatiuk (2006); Parks (2006); Hertam (2010)	Decrease	Yes	9	5	1	1	2

Weighting system as per Table 3. For each freshwater ecosystem component, the hypothesized effect is indicated in parentheses.

amphibians, and no laboratory experiments were conducted on waterfowl. Field experiments provided support for the hypotheses of an increase in nitrogen, phosphorus and phytoplankton/chlorophyll *a* and of a decrease in aquatic macrophytes, benthic invertebrates, and amphibians, but there was inconsistent evidence for impacts on turbidity and zooplankton, and insufficient evidence for an impact on waterfowl and fish. Finally, natural experiments supported the hypothesis of an increase in turbidity/suspended solids, nitrogen, and phosphorous and a decrease in macrophytes and fish, but provided insufficient evidence for other impacts, even though they never resulted in inconsistent evidence. In no case was a conclusion reached by either laboratory, field, or natural experiments in support of the alternative hypothesis.

Component-wise, evidence for an impact was available from either laboratory, field, or natural experiments for turbidity/solids, nitrogen, phosphorus, phytoplankton/chlorophyll *a*, benthic invertebrates, amphibians, and fish. Field and natural experiments provided evidence for nitrogen, phosphorus and aquatic macrophytes (Table 9). Whereas, inconsistent (field and laboratory) and insufficient evidence (natural experiments) were provided for impacts on zooplankton, but there was insufficient evidence for impacts on waterfowl due to the very low number of studies.

As a result of the above conclusions and based on the total outcome scores, the relative strength of overall experimental evidence for an impact was: "very high" (score = 5) for nitrogen, phosphorus, and aquatic macrophytes; "high" (3) for turbidity/suspended solids, fish, and benthic invertebrates; "moderate" (2) for phytoplankton/chlorophyll *a* and amphibians. Whereas, there was "inconsistent evidence" (0) for impacts on zooplankton, and "insufficient evidence" for impacts on waterfowl (Table 9, Figure 6).

Biomass

Biomass values for carp having an effect on a certain component were provided by 73 experiments in total (Table 5). Of these, 34 (45.3%) were conducted in the laboratory, another 34 (45.3%) in the field and 7 (9.4%) under natural conditions. The range in biomass values across all components was very wide (18–19 375 kg ha^{-1}) and also when broken down across individual components for water quality, vegetation, and invertebrates, but not for vertebrates likely due to the lower number of studies (Figure 7A). Similarly, the range in values was wider for laboratory and field compared to natural experiments (Figure 7B), but less so between 0+ and 1+ and older fish (Figure 7C). However, the upper limit of all these ranges was mainly influenced by the biomass values used in the series of experiments by Angeler et al. (2002a,b; 2007) and Angeler and Rodrigo (2004) as well as by those of Wells (2013) and Fischer et al. (2013), all relying on very high carp stocking densities (Table 5). For this reason, biomass values from these experiments were regarded as outliers and dropped from the statistical estimation of critical biomass (i.e., threshold) for causing an impact.

There were statistically significant differences both amongst component groups (but not between/amongst individual components within each group) and experimental locations, but no differences between fish ages (Table 10). Specifically, mean critical biomass for an impact on water quality and vegetation was higher relative to that for invertebrates and vertebrates, with no significant differences within the two groups; whereas, there were no differences between vertebrates and invertebrates (Figure 7D). Based on experimental location, mean critical biomass was significantly higher for field relative to laboratory and natural experiments, which did not differ significantly (Figure 7E). Whereas, there were

Table 7 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for natural experiments (ordered according to Table 1)

				Study details	
Citation	Effect	Support	Weight	Study design	Sampling units
Turbidity/Suspended solids	(Increase)				
Fletcher et al. (1985)	None	No	4	After impact only	0 (control); 4 (impacted)
Bowmer et al. (1994)	Increase	Yes	4	Reference/control vs. impact (no before)	1 (control); 1 (impacted)
Fernández et al. (1998)	Increase	Yes	4	After impact only	0 (control); 34 (impacted)
Lougheed et al. (1998)	Increase	Yes	8	Reference/control vs. impact (no before)	8 (control); 11 (impacted)
Chow-Fraser (1999)	Increase	Yes	4	After impact only	0 (control); 4 (impacted)
Zambrano et al. (1999)	Increase	Yes	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Barton et al. (2000)	Increase	Yes	7	Before vs. after (no reference/control)	1 (control); 3 (impacted)
Beklioğlu et al. (2000)	Increase	Yes	1	After impact only	0 (control); 1 (impacted)
Rowe (2007)	Increase	Yes	10	BACI or BARI MBACI or Beyond MBACI	40 (control); 9 (impacted)
Stewart and Downing (2008)	Increase	Yes	7	Reference/control *vs.* impact (no before)	7 (control); 2 (impacted)
Jackson et al. (2010)	Increase	Yes	9	Gradient response model	129 (independent)
Weber and Brown (2011)	Increase	Yes	9	Gradient response model	81 (independent)
Nitrogen	(Increase)				
Bowmer et al. (1994)	Increase	Yes	4	Reference/control vs. impact (no before)	1 (control); 1 (impacted)
Zambrano et al. (1999)	None	No	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Beklioğlu et al. (2000)	Increase	Yes	1	After impact only	0 (control); 1 (impacted)
Jackson et al. (2010)	Increase	Yes	9	Gradient response model	129 (independent)
Weber and Brown (2011)	Increase	Yes	9	Gradient response model	81 (independent)
Phosphorus	(Increase)				
Bowmer et al. (1994)	Increase	Yes	4	Reference/control vs. impact (no before)	1 (control); 1 (impacted)
Meredith et al. (1995)	None	No	4	After impact only	0 (control); 26 (impacted)
Zambrano et al. (1999)	None	No	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Beklioğlu et al. (2000)	Increase	Yes	1	After impact only	0 (control); 1 (impacted)
Jackson et al. (2010)	Increase	Yes	9	Gradient response model	129 (independent)
Weber and Brown (2011)	Increase	Yes	9	Gradient response model	81 (independent)
Phytoplankton/Chlorophyll *a*	(Increase)				
Zambrano et al. (1999)	None	No	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Beklioğlu et al. (2000)	Increase	Yes	1	After impact only	0 (control); 1 (impacted)
Weber and Brown (2011)	Increase	Yes	9	Gradient response model	81 (independent)
Aquatic macrophytes	(Decrease)				
Fletcher et al. (1985)	Change	No	4	After impact only	0 (control); 4 (impacted)
Fernández et al. (1998)	Decrease	Yes	4	After impact only	0 (control); 34 (impacted)
Lougheed et al. (1998)	Decrease	Yes	8	Reference/control vs. impact (no before)	8 (control); 11 (impacted)
Zambrano et al. (1999)	Decrease	Yes	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Titus et al. (2004)	Decrease	Yes	1	After impact only	0 (control); 1 (impacted)
Beklioglu et al. (2006)	Decrease	Yes	7	Reference/control vs. impact (no before)	3 (control); 2 (impacted)
Britton et al. (2007)	Increase	No	1	After impact only	0 (control); 1 (impacted)
Bajer et al. (2009)	Decrease	Yes	1	After impact only	0 (control); 1 (impacted)
Zooplankton	(Change)				
Zambrano et al. (1999)	None	No	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Beklioğlu et al. (2000)	Decrease	Yes	1	After impact only	0 (control); 1 (impacted)
Benthic invertebrates	(Decrease)				
Zambrano et al. (1999)	Decrease	Yes	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)
Stewart and Downing (2008)	Decrease	Yes	7	Reference/control vs. impact (no before)	7 (control); 2 (impacted)
Amphibians	(Decrease)				
Zambrano et al. (2010)	Decrease	Yes	4	After impact only	0 (control); 20 (impacted)
Waterfowl	(Decrease)				
Bajer et al. (2009)	Decrease	Yes	1	After impact only	0 (control); 1 (impacted)
Caithamer (2012)	Decrease	Yes	1	After impact only	0 (control); 1 (impacted)
La Porte et al. (2014)	Decrease	Yes	2	Before vs. after (no reference/control)	0 (control); 1 (impacted)
Fish	(Decrease)				
Swar and Gurung (1988)	Decrease	Yes	2	Before vs. after (no reference/control)	0 (control); 1 (impacted)
Miller and Beckman (1996)	Decrease	Yes	4	After impact only	0 (control); 3 (impacted)
Specziár et al. (1998)	Decrease	Yes	4	After impact only	0 (control); 3 (impacted)
Zambrano et al. (1999)	None	No	8	Reference/control vs. impact (no before)	4 (control); 8 (impacted)

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Table 7 Evidence for each of the ten cause–effect linkages relating carp to freshwater ecosystems (Table 2) at the individual assessment level for natural experiments (ordered according to Table 1) *(Continued)*

Citation	Effect	Support	Weight	Study details	
				Study design	Sampling units
Egertson and Downing (2004)	Change	No	9	Gradient response model	32 (independent)
Cardona et al. (2008)	Decrease	Yes	6	Reference/control vs. impact (no before)	1 (control); 2 (impacted)
Jackson et al. (2010)	Decrease	Yes	9	Gradient response model	129 (independent)
Weber and Brown (2011)	Decrease	Yes	9	Gradient response model	81 (independent)
Mazumder et al. (2012)	Decrease	Yes	4	After impact only	0 (control); 3 (impacted)
Andreu-Soler and Ruiz-Campos (2013)	Decrease	Yes	3	After impact only	0 (control); 2 (impacted)

Weighting system after Webb et al. (2013). For each freshwater ecosystem component, the hypothesized effect is indicated in parentheses.

no statistically significant differences between age groups (Figure 7F). Based on these findings, the following critical biomass values were estimated: 546 ± 50 kg ha^{-1} (mean ± SE) for water quality and vegetation combined, and 304 ± 39 kg ha^{-1} for invertebrates and vertebrates combined; 567 ± 68 kg ha^{-1} for field experiments and 409 ± 42 kg ha^{-1} for both laboratory and natural experiments; and 476 ± 38 kg ha^{-1} overall.

By including only critical biomass values from experiments on "free-ranging" carp, the estimated biomass threshold for

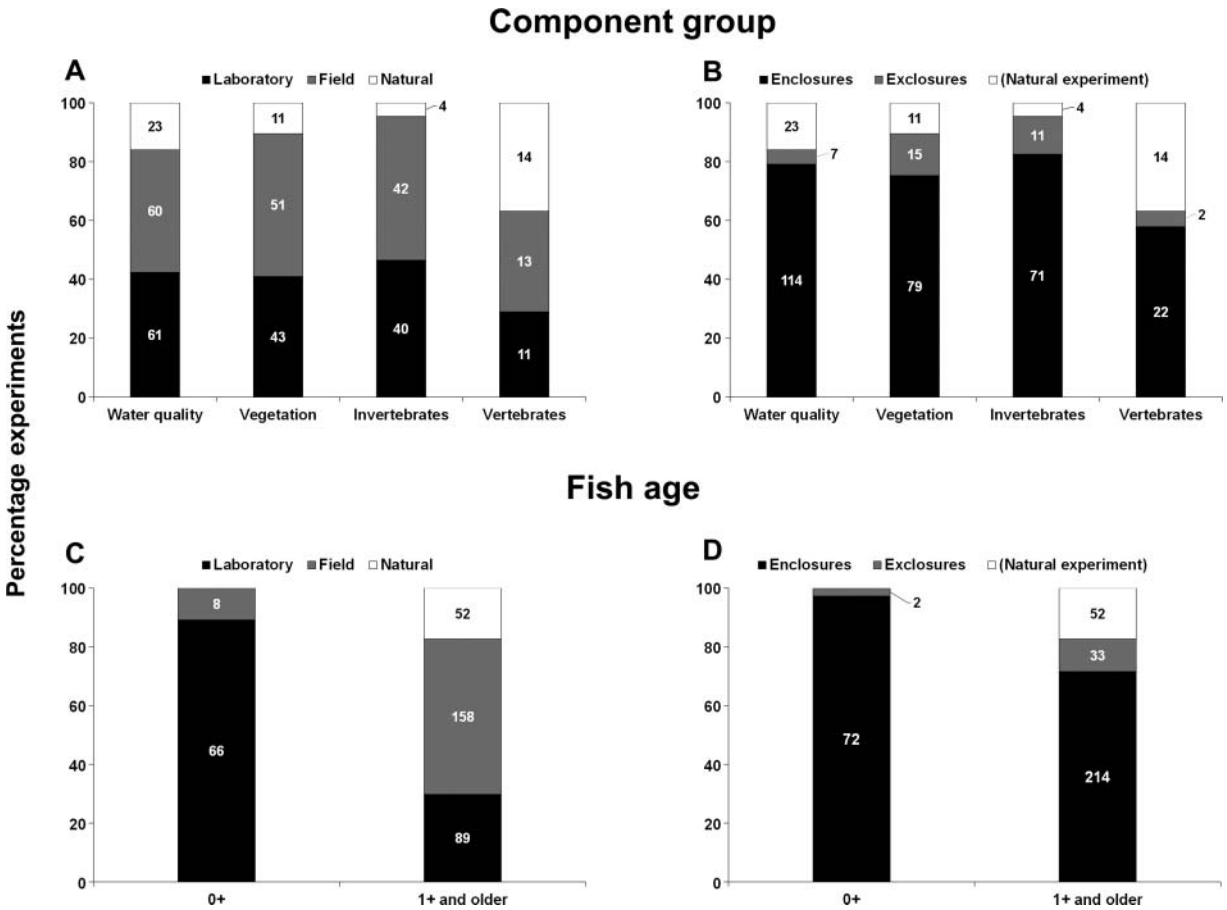

Figure 3 (A) Proportion of assessments (with sub-totals) based on laboratory, field, and natural experiments evaluating the effects of carp on four freshwater ecosystem component groups. Water quality: turbidity/suspended solids, nitrogen, and phosphorus; vegetation: phytoplankton/chlorophyll *a*, aquatic macrophytes; macroinvertebrates: zooplankton and benthic invertebrates; vertebrates: amphibians, waterfowl, and fish. (B) Proportion of assessments (with sub-totals) based on enclosures, exclosures or "plot-free" (i.e., natural experiments) to evaluate the effects of carp on the four component groups. (C) Proportion of assessments (with sub-totals) based on laboratory, field, and natural experiments evaluating the effects of 0+ and 1+ and older carp on freshwater ecosystems (pooled components) (see Table 5). (D) Proportion of assessments (with sub-totals) based on different plot types the effects of 0+ and 1+ and older carp on freshwater ecosystems (pooled components).

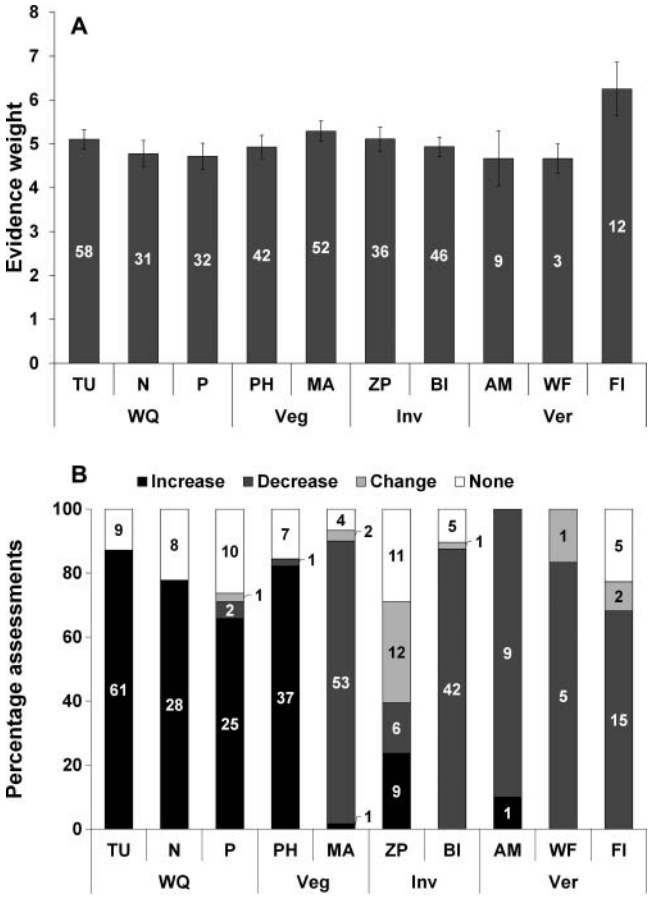

Figure 4 (A) Mean evidence weight (± SE) of laboratory- and field-based assessments (with sub-totals) evaluating the effects of carp on 10 freshwater ecosystem components. Computation of evidence weights as per Table 3. Component groups as per Figure 3. TU = turbidity/suspended solids; N = nitrogen; P = phosphorus. Biotic components: PH = phytoplankton/chlorophyll *a*; MA = aquatic macrophytes; ZP = zooplankton; BI = benthic invertebrates; AM = amphibians; WF = waterfowl; FI = fish. (B) Proportion of assessments detecting an increase, decrease, change, or no variation on each of the ten components (see Table 5).

carp having an effect across the freshwater ecosystem components under investigation was 198 ± 40 kg ha^{-1} (Figure 8). This overall value could be set given the lack of statistically significant differences either amongst components groups ($F_{3,12} = 0.98$, $P_{\text{permutational}} = 0.418$) or amongst/individual components therein ($F_{5,12} = 0.04$, $P_{\text{permutational}} = 0.999$), with the notable exception of amphibians for which no biomass values were available (Table 5).

DISCUSSION

History and Biogeography

This review has shown how, over the past nine decades, studies evaluating the effects of carp on freshwater ecosystems have relied on a broad gamut of experimental settings. These have included laboratory, field, and natural locations in combination with various types of arena, and with carp either confined within enclosures or free ranging. Also, implementation of the reviewed experiments in some 19 countries across five continents reflects the global interest on the environmental biology of this species and, in several cases, the concerns about its potential impacts on freshwater ecosystems.

Not surprisingly, the majority of experiments were carried out in countries of North America and Australasia categorized as high risk, with the first experiments undertaken between the 1940s and 1970s in the United States and later between the 1990s and 2000s in Canada (but see Macrae, 1979). This is in agreement with the first historical accounts from the United States of the detrimental effects of carp on water quality, aquatic vegetation and, possibly, fish (Cole, 1905; Cahn, 1929), and with the first extensive report on the species' noxiousness in Canadian fresh waters (McCrimmon, 1968). On the contrary, in Australia, following two decades of mounting concerns about the spread and establishment of the "Boolara" strain of carp across the Murray-Darling Basin (Butcher, 1962; Forsyth et al., 2013), experimentation started in the 1980s and flourished from the 1990s onward, with emphasis placed on the species' detrimental impacts on the floodplain wetlands typical of the region. Finally, in New Zealand the accidental release of ornamental "nishikigoi" or "koi" (redundantly, "koi carp": Balon, 2004) into the Waikato River basin in the 1960s and its subsequent spread into adjacent water bodies has recently stimulated experimental investigations, also aimed to assist in implementation of biomanipulation measures (Burns et al., 2014).

By contrast, in Europe (including Turkey) there has been historically an overall mixed attitude toward carp (Copp et al., 2005; Savini et al., 2010; Vilizzi, 2012). This is because the species is native to parts of the Old Continent and Black Sea tributaries (namely, the western dispersant *C. c. carpio* found east of the piedmont zone flood plain of the River Danube through to the Aral Sea: Balon, 1995) and was introduced throughout the rest of Europe from Roman times (Balon, 1995), during the Medieval Ages (Hoffmann, 1995), and until the 19th century (Copp et al., 2005). So imbedded is this "cultural" perception of the carp (Spates, 2013) that the species is ignored in the non-native species legislation of some, if not several, European countries where the species was introduced centuries ago (Copp et al., 2005). Indeed, in the United Kingdom, a review of non-native fisheries (Hickley and Chare, 2004) did not include common carp amongst its several case studies, and the only mention of the species was with reference to its increasing popularity amongst anglers (e.g., 36% of anglers responding to a questionnaire named carp as their preferred target species). These contrasting levels of public perception and scientific concern about carp have involved different rationales and scopes for conducting experimental research, and this was reflected in the categorization of the eight European countries for which experiments were reviewed into "no," "low," and "medium" risk.

Table 8 Risk-based categorization of the countries for which experimental data on carp effects on freshwater ecosystems were reviewed

Risk	Outcome score	Country	Continent	Criteria: Status	Criteria: Invasiveness	Criteria: Public perception	Criteria: Scientific concern	Sample reference(s)
No	0	Hungary	Europe	Native	None	Positive	None	Bakos and Gorda (2001); Specziár and Turcsányi (2015)
Low	2	Poland	Europe	Naturalized	None	Positive	None	Szücs et al. (2007); Nieoczym and Kloskowski (2014, 2015)
Low	3	Turkey	Europe	Semi-native	Low	Positive	Low	Vilizzi (2012); Tarkan et al. (2014)
Low	4	China	Asia	Semi-native	Moderate	Positive	Low	Yan et al. (2001); Tang and Chen (2012)
Low	4	Germany	Europe	Naturalized	Low	Positive	Low	Barthelmes and Brämick (2003); Arlinghaus and Mehner (2003)
Medium	5	France	Europe	Naturalized	Low	Indifferent	Low	Crivelli (1983); Poizat and Crivelli (1997)
Medium	5	Japan	Asia	Semi-native	Moderate	Positive	Moderate	Matsuzaki et al. (2007); Uchii et al. (2013)
Medium	5	Netherlands	Europe	Naturalized	Low	Indifferent	Low	ten Winkel and Meulemans (1984)
Medium	5	Nigeria	Africa	Alien	Low	Indifferent	None	Olaniyan (1961); Barker (1994)
Medium	5	United Kingdom	Europe	Naturalized	Low	Positive	Moderate	Britton et al. (2010); Copp et al. (2015a)
Medium	6	Nepal	Asia	Alien	Low	Indifferent	Low	Swar and Gurung (1988); Gurung (2007)
Medium	7	Argentina	South America	Alien	Moderate	Indifferent	Low	Fernández et al. (1998)
Medium	8	Kenya	Africa	Alien	Moderate	Indifferent	Moderate	Britton et al. (2007); Oyugi et al. (2014)
Medium	8	Mexico	North America	Alien	Moderate	Indifferent	Moderate	Tapia and Zambrano (2003); Zambrano et al. (2006)
Medium	8	Spain	Europe	Naturalized	High	Indifferent	Moderate	Almeida et al. (2013); Clavero and Villero (2014)
High	10	New Zealand	Australasia	Alien	Moderate	Negative	High	Hanchet (1990); Rowe (2007)
High	11	Australia	Australasia	Alien	High	Negative	High	Koehn (2004); Vilizzi and Copp (2013)
High	11	Canada	North America	Alien	High	Negative	High	McCrimmon (1968); Badiou and Goldsborough (2006)
High	11	United States	North America	Alien	High	Negative	High	Cahn (1929); Moyle (1984)

Outcome score for each country is computed as the sum of the partial scores for each criterion as follows: Status = 0 (native; Froese and Pauly 2014; also, Chistiakov and Voronova 2009), 1 (semi-native: i.e., native to some areas of the country but translocated/introduced elsewhere), 2 (naturalized: i.e., long-established, self-sustaining populations: Copp et al., 2005), 3 (alien: i.e., introduced in relatively recent times, established and invasive); invasiveness (based on number/extent of invaded areas) = 0 (none), 1 (low), 2 (moderate), and 3 (high); public perception = 0 (positive: e.g., cultural, historical, and sport fishing value), 1 (indifferent: e.g., mostly unnoticed, public awareness still lacking), 2 (negative: e.g., undesired, unpalatable, "vermin," to some extent also anecdotally). Scientific concern (based on number/extent of reports on demonstrated/putative impacts) = 0 (none), 1 (low), 2 (moderate), and 3 (high).

Availability of only one experiment from the sole (no-risk) country in the reviewed dataset where carp is native (i.e., Hungary) reflected the species' local aquacultural and farming value (Specziár and Turcsányi, 2015). Similarly, in (low-risk) Poland and Germany, where naturalized carp is widely appreciated for aquaculture (Szücs et al., 2007) and sport fishing (Arlinghaus and Mehner, 2003), experiments have mainly focused on habitat enhancement for fisheries and amenity value. Conversely, in Turkey (the other low-risk European country) carp is native to several ecoregions (Vilizzi, 2012) and overall ubiquitous as a result of intensive translocations (Innal and Erk'akan, 2006). Yet, despite carp representing a highly productive fishery (Harlioğlu, 2011; Turkish Statistical Institute, 2012) and being generally well perceived by the public (Vilizzi, 2012), likely detrimental effects on the water quality and native fauna of some shallow lakes have recently stimulated experimental studies and biomanipulation efforts, further supported by a risk-based reassessment of the species' invasiveness potential (Tarkan et al., 2014).

Of the other four European countries, France, the Netherlands, and the United Kingdom achieved the same outcome score (i.e., bottom of the medium-risk range) due to naturalized carp being perceived by the public as "indifferent" in the former two countries, but being highly valued for sport fishing in the United Kingdom (despite increasing evidence for impacts on some amenity and conservation values). Whereas, Spain achieved a score located at the top of the range. Thus, the oft-cited study by Crivelli (1983), which was meant to replicate under Mediterranean conditions the findings from North American experiments of aquatic macrophyte destruction by carp, reported comparatively less severe impacts likely due to different resource availability. Similarly, the majority of experiments carried out in the Netherlands used carp mainly as a representative benthivorous/predatory cyprinid for investigating bottom-up and top-down processes in lake ecosystems.

Conversely, in the United Kingdom, where carp was formerly appreciated as a palatable and "widely respected" species (Spates, 2013) and is currently highly valued for sport fishing (Hickley and Chare, 2004), a reassessment of its potential impacts (Moss et al., 2002) is under way in response to legislative obligations to implement the EU Water Framework Directive (http://ec.europa.eu/environment/water/water-framework/index_en.html, 16 June

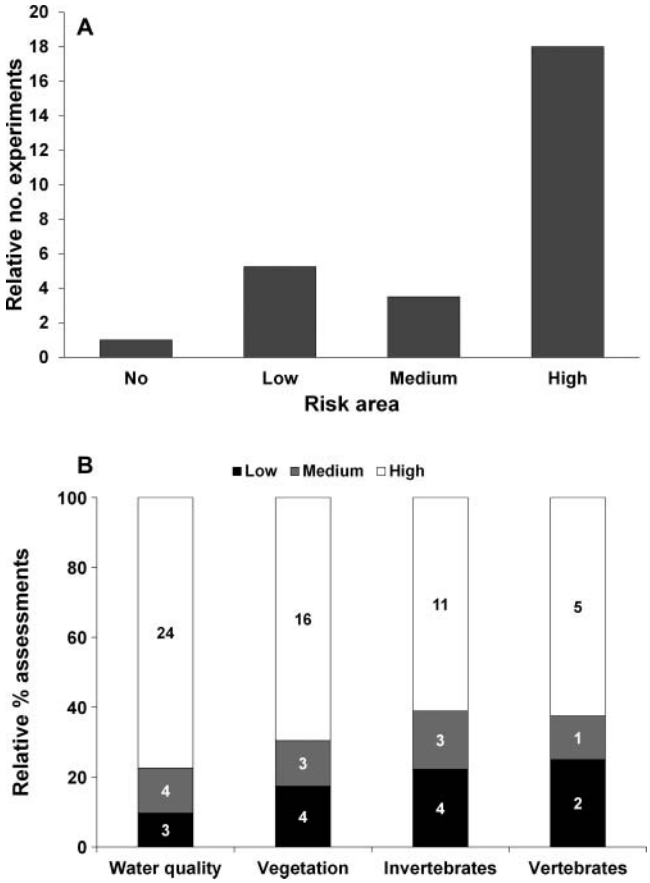

Figure 5 (A) Relative number of experiments (i.e., total divided by number of countries per risk area: Table 8) evaluating carp effects on freshwater ecosystems. (B) Relative proportion of assessments (with sub-totals) for low, medium, and high risk areas on the four component groups (see also Table 5).

2015) and the EU Regulation on the use of aliens in aquaculture (Copp et al., 2015a). This scientific attitude was well represented in the UK-based multi-component field experiments investigating the top-down and bottom-up processes related to carp impacts, with a view to prospective restoration programmes. Finally, the higher outcome score for Spain (and, overall, for the whole Iberian Peninsula), in spite of carp being naturalized in the region, was mainly due to the species' rapid spread in recent decades brought about by river regulation and impoundments, and also facilitated by the Mediterranean climate conditions of the area. All of these factors have recently contributed to increased concerns about the severity of carp impacts (Almeida et al., 2013; Clavero and Villero, 2014), thereby fostering experimentation.

Similar to Europe, the eastern dispersant *C. carpio haematopterus* (the Amur wild carp: Chistiakov and Voronova, 2009) is native to several parts of Asia but has been translocated across or introduced to several countries therein (Froese and Pauly, 2014). Thus, categorization of China as low risk was a result of overall low scientific concern, with experiments focusing mainly on the use of carp as a biological control agent and with limited concerns about its effects on the ecosystem "if properly managed" (Wong et al., 2009). Notably, this approach was similar for Argentina, where experiments on alien carp were conducted mainly to assess its effectiveness for invasive weed control programmes. On the other hand, multi-tiered, field-based experimental studies are now being undertaken in Japan following recent findings of wild carp that display marked behavioral, morphological and physiological differences relative to its non-native counterpart (Matsuzaki et al., 2009b; Ito et al., 2014); this coinciding with the increasingly threatened status of the wild form in some areas of distribution (Mabuchi et al., 2008; Uchii et al., 2013).

Of the remaining four medium-risk countries, the comparatively lower scores achieved for Nigeria and Nepal were an outcome of the species' low invasiveness and limited scientific concern, which were reflected by the paucity of experimental studies. Conversely, the higher score values for Kenya and Mexico resulted from increasing awareness of the potential spread and detrimental effects of carp in these areas, leading to extensive experimentation (especially in Mexico) as well as development of generalized predictive models of impact and invasive potential (Zambrano et al., 2001, 2006; Jackson et al., 2012).

Risk Areas

For proper evaluation of carp effects (including its impacts) it is critical to define the context in which these are going to be of relevance, which in the present case will be by nation state rather than by biogeographical regions. As a result, the consequences of documented/potential carp impacts will become of relevance not only to the high-risk countries (for which additional scientific support was provided by the current findings) but also to a range of countries in which mounting concerns have been manifested about the risks associated with potential further carp spread. Clearly, the present evaluation will ultimately have to be gauged at the "higher decision-making echelons" so as to ensure proper balance between ecological requirements for habitat conservation and pressing economic demands (Copp et al., 2005; Gozlan, 2008; Britton and Gozlan, 2013).

Overall, and perhaps somewhat paradoxically, the establishment of carp in 91 of the 120 countries where it was introduced (Casal, 2006) belittles the number of countries where experiments have been carried out. However, because introduction and establishment of a non-native fish species does not necessarily result in an impact (Gozlan, 2008), it is envisaged that no additional measures other than prevention and early detection (Britton et al., 2011a,b) may be required in those cases where an overall assessment of the carp status in newly colonized areas has already been made and no significant risks have been identified (e.g. Brazier et al., 2012). In this respect, a review for the Mediterranean Region found that studies in only three (i.e., Turkey, Israel, and Algeria) of 18 countries reported "circumstantial" evidence of detrimental

Table 9 Results of causal criteria analysis for the ten hypotheses about carp effects on freshwater ecosystems

Component	Score	Trajectory	Experiment	Conclusion	Number of evidence items			Summed weights		
					Total	In favor	Against	Total	In favor	Against
Abiotic										
Water quality										
Turbidity	3	Increase	*Laboratory*	*Inconsistent evidence*	*27*	*24*	*3*	*157*	*136*	*21*
			Field	*Inconsistent evidence*	*31*	*26*	*5*	*139*	*117*	*22*
			Natural	**Support for hypothesis**	**12**	**11**	**1**	**71**	**67**	**4**
Nitrogen	5	Increase	*Laboratory*	*Inconsistent evidence*	*16*	*12*	*4*	*83*	*54*	*29*
			Field	**Support for hypothesis**	**15**	**12**	**3**	**65**	**53**	**12**
			Natural	**Support for hypothesis**	**5**	**4**	**1**	**31**	**23**	**8**
Phosphorus	5	Increase	*Laboratory*	*Inconsistent evidence*	*18*	*12*	*6*	*91*	*57*	*34*
			Field	**Support for hypothesis**	**14**	**9**	**5**	**60**	**42**	**18**
			Natural	**Support for hypothesis**	**6**	**4**	**2**	**35**	**23**	**12**
Biotic										
Vegetation										
Phytoplankton/chlorophyll *a*	2	Increase	*Laboratory*	*Inconsistent evidence*	*21*	*17*	*4*	*112*	*87*	*25*
			Field	**Support for hypothesis**	**21**	**18**	**3**	**95**	**79**	**16**
			Natural	Insufficient evidence	3	2	1	18	10	8
Aquatic macrophytes	5	Decrease	*Laboratory*	*Inconsistent evidence*	*22*	*19*	*3*	*126*	*106*	*20*
			Field	**Support for hypothesis**	**30**	**28**	**2**	**149**	**140**	**9**
			Natural	**Support for hypothesis**	**8**	**6**	**2**	**34**	**29**	**5**
Invertebrates										
Zooplankton	0	Change	*Laboratory*	*Inconsistent evidence*	*20*	*16*	*4*	*115*	*89*	*26*
			Field	*Inconsistent evidence*	*16*	*10*	*6*	*69*	*40*	*29*
			Natural	Insufficient evidence	2	1	1	9	1	8
Benthic invertebrates	1	Decrease	**Laboratory**	**Support for hypothesis**	**20**	**17**	**3**	**103**	**85**	**18**
			Field	**Support for hypothesis**	**26**	**22**	**4**	**124**	**105**	**19**
			Natural	Insufficient evidence	2	2	0	15	15	0
Vertebrates										
Amphibians	2	Decrease	Laboratory	Insufficient evidence	1	1	0	4	4	0
			Field	**Support for hypothesis**	**8**	**7**	**1**	**38**	**35**	**3**
			Natural	Insufficient evidence	1	0	1	4	4	0
Waterfowl	?	Decrease	Laboratory	–	—	—	—	—	—	—
			Field	Insufficient evidence	3	2	1	14	10	4
			Natural	Insufficient evidence	3	3	0	5	5	0
Fish	3	Decrease	*Laboratory*	*Inconsistent evidence*	*10*	*6*	*4*	*61*	*33*	*28*
			Field	Insufficient evidence	2	1	1	14	9	5
			Natural	**Support for hypothesis**	**10**	**8**	**2**	**58**	**41**	**17**

For laboratory and field experiments, the weighting system is based on an evaluation of robustness as per Table 2; whereas, for natural experiments the Eco Evidence weighting system of Webb et al. (2013) was used. For each component, the total outcome score is computed as the sum of weights of conclusion × location of experiment combinations (see Table 4). In bold, conclusions supporting the hypothesis; in italics, conclusions resulting in inconsistent evidence. Note that for waterfowl the outcome score of 0 is replaced by a question mark (?) because of insufficient evidence. Evidence for each cause–effect linkage at the individual assessment level in Table 6 (laboratory and field experiments) and Table 7 (natural experiments). See also Figure 6.

impacts by carp, and only two studies provided "experimental" evidence for such impacts (Beklioğlu et al., 2000, 2006). In such cases, empirical predictive models could be considered (e.g., Coates and Ulaiwi, 1995), or reconnaissance-based assessments carried out to monitor the early stages of invasion (e.g., Troca et al., 2012) and/or estimate carp abundance relative to that of the native species (e.g., Olds et al., 2011; Alexandar and Siva Sankar, 2013; Choudhury et al., 2013).

Specific to the countries in the present study (and excluding those categorized as high risk, for which management and control measures are already in place), containment of semi-native carp where already present may be all that is required in water bodies of China and Japan, where overall localized impacts have already been reported. Conversely, in Turkey stocking of semi-native carp into additional man-made reservoirs, other than those where the species is already present (Çetinkaya, 2010), may still be feasible. This is because further stocking would likely result in little or no ecologically meaningful impacts on the native fauna, provided that preventative measures are adopted to avoid accidental, concomitant introductions of truly noxious non-native species (Tarkan et al., 2014). This contention was recently supported by evidence for negative allometric growth and overall lower growth rates for carp in Anatolia compared to native and invaded areas worldwide, which was attributed to a combination of the lower genetic resilience of the more widespread mirror variety relative to the fully scaled variant and the less suitable spawning habitats provided by man-made reservoirs (Vilizzi et al., 2013a, 2015).

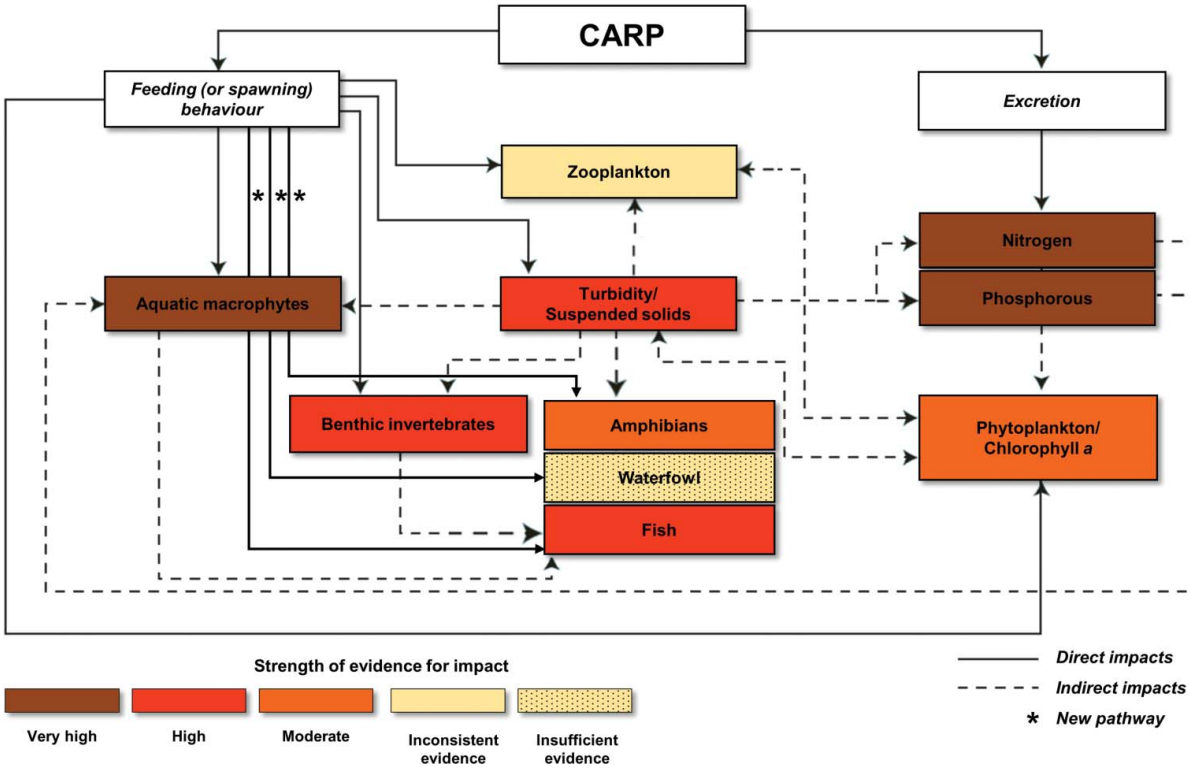

Figure 6 Conceptual model (updated from Koehn et al., 2000) of the effects of carp on freshwater ecosystems. Relative strength of evidence for impacts for each component is based on a total outcome score computed from the sum of weights of conclusions based on the location of experiments (see Table 9). Note that nitrogen and phosphorus are part of "nutrients," and amphibians, waterfowl and fish of the "other native fauna" grouping in Koehn et al.'s (2000) original model. (Color figure available online.)

On the other hand, in the United Kingdom and Spain (Iberia), management actions to avoid further spread of naturalized carp and population control/eradication campaigns in water bodies of conservation interest, respectively, are likely to be necessary given available experimental evidence and recent risk assessments (Almeida et al., 2013; Copp et al., 2015a). Finally, in Argentina, Kenya, and Mexico, where carp was introduced only relatively recently, careful evaluation should be made of the risks associated with potential larger scale spread and establishment across pristine water bodies, which are likely to be more prone to carp invasion, especially in the light of the aforementioned modeled projections and documented disastrous consequences experienced in the United States, Canada, and Australia.

With regard to the other countries, except for Hungary where measures for conservation of native carp are relevant (Balon, 1995; Koščo and Holčík, 2008), informed decisions on a case-by-case basis should still be considered as part of wider pan-European risk assessments (e.g., Copp et al., 2015b), and the general guidelines provided above are likely to apply. However, it remains to be evaluated to what extent the precautionary ("guilty until proven innocent") approach advocated by some (e.g., Savini et al., 2010) would be fully defensible. This is because perceived socio-economic benefits may, and in some cases do, ultimately prevail over ecological concerns.

Impacts

The "tens" rule notwithstanding (Gozlan, 2008), there is little if any doubt that carp introductions worldwide have resulted in significant ecological impacts, i.e., in measurable losses of diversity or change in ecosystem function (Gozlan et al., 2010). Indeed, as an "exotic ecosystem engineer" (Crooks, 2002), introduced carp can incite profound changes in aquatic ecosystems, and the reviewed experiments were overall in agreement as to the extent of carp impacts on almost all of the ecological components under investigation. However, there were some exceptions to this, specifically where no effect or no change were detected, being contrary to expectation.

In the case of no effect (excluding the possibility of a real absence of an effect, i.e., true null hypothesis), low power issues in the design of (an unquantified number of) experiments cannot be ruled out (Kirk, 2013). In fact, none of the reviewed experiments, except for that by Vilizzi et al. (2014b), provided (at least explicitly) an *a priori* power analysis (e.g., to justify the number of treatment and/or control replicates to be employed). However, Matsuzaki et al. (2009a) did estimate *a posteriori* the effect size of 16 experiments on the effects of carp on a subset of the components examined in the present study and, except for

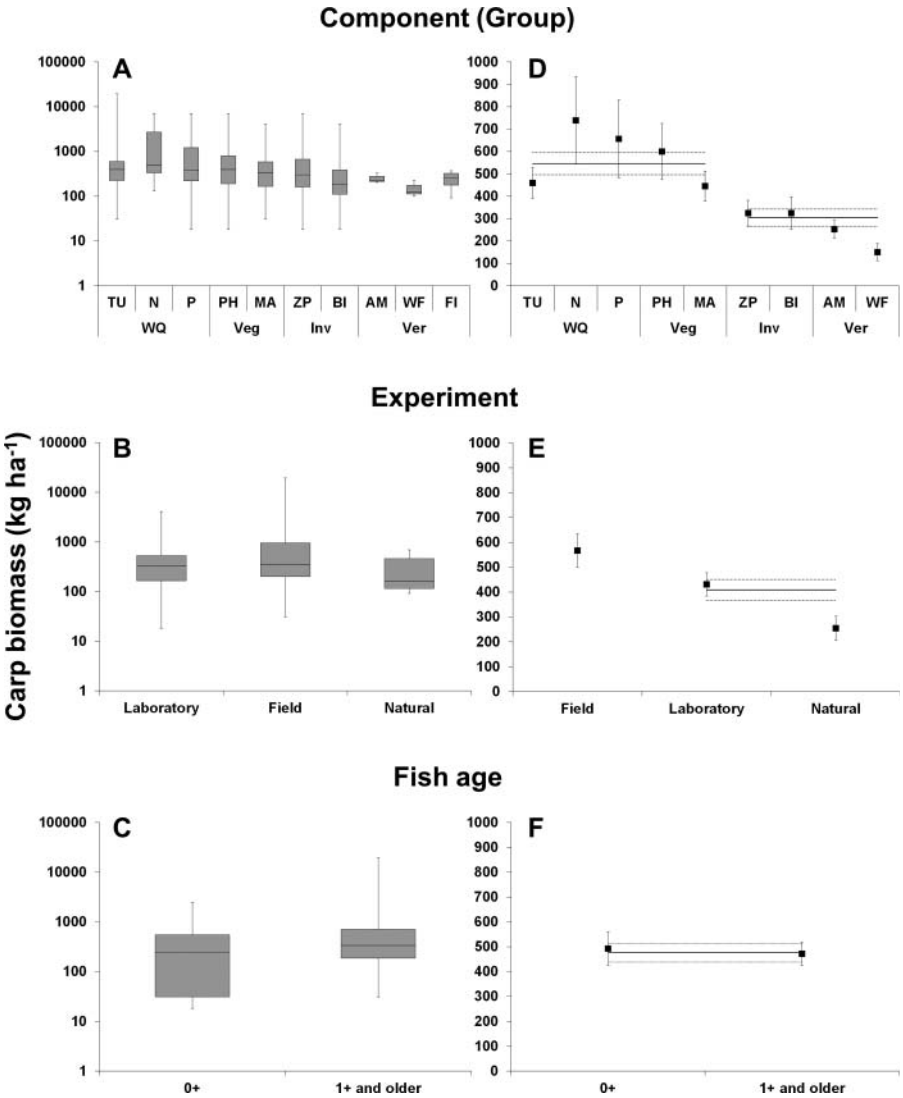

Figure 7 (Left column) Box-and-whisker plots (25th, 50th, and 75th percentile; log scale) for carp biomass having an effect (positive, negative, or change) on freshwater ecosystems: (A) across the 10 component groups (WQ = water quality; Veg = vegetation; Inv = invertebrates; Ver = vertebrates) and the individual components therein under investigation (TU = turbidity/suspended solids; N = nitrogen; P = phosphorus; PH = phytoplankton/chlorophyll *a*; MA = aquatic macrophytes; ZP = zooplankton; BI = benthic invertebrates; AM = amphibians; WF = waterfowl; FI = fish); (B) based on experimental location; and (C) according to fish age. (Right column) Mean (± SE) biomass (after outlier removal) for carp having an impact: (D) on the components groups and components under investigation, with overall mean ± SE biomass values (solid and hatched lines, respectively) for water quality/vegetation and invertebrates/vertebrates components; (E) based on experimental location, with overall mean ± SE biomass values for field and natural/experiments; and (F) according to fish age, with global mean ± SE biomass value. See also Table 10 for PERANOVA results.

one experiment, were able to confirm statistically significant effects.

Decreases were observed, where increases were expected, in some assessments of phosphorus and phytoplankton, and these were attributed to rapid uptake by periphyton and cyanobacteria (Matsuzaki et al., 2007, 2009a) and to increased levels of turbidity (Wahl et al., 2011), respectively. An increase instead of a decrease was reported in two cases, namely, for aquatic macrophytes and for amphibians, and these were ascribed to invasive carp displacing invasive crayfish (Britton et al., 2007) and selectively consuming predatory invertebrates upon tadpoles (Denton and Beebee, 1997), respectively. In the former case, the validity of finding (which was regarded as an unexpected outcome) was reported as subject to further, long-term evaluation, and more recently reinterpreted in terms of serial replacement of invasive species theory (Jackson et al., 2012). In the latter case, the outcome effectively resulted from a carp impact on a related component (i.e., benthic invertebrates), hence confirming the species' overall detrimental effects on the freshwater ecosystem community in general.

Except for zooplankton, a change was detected for a number of components, including phosphorus, aquatic macrophytes, benthic invertebrates, waterfowl, and fish. Thus, sediment characteristics were deemed responsible for the

Table 10 PERANOVA results showing differences in carp biomass (with outlier values removed) having an impact on freshwater ecosystems based on the 10 component groups and individual components therein (water quality: turbidity/solids, nitrogen, and phosphorus; vegetation: phytoplankton/chlorophyll *a*, aquatic macrophytes; macroinvertebrates: zooplankton and benthic invertebrates; vertebrates: amphibians, waterfowl, and fish), laboratory, field, or natural experiments, and according to fish age (0+ and 1+ and older)

Source	d*f*	MS	$F^{\#}$	$t^{\#}$	$P^{\#}$
Group	3	4.14	4.35		**0.007**
Water quality vs. vegetation	1			1.17	0.244
Water quality vs. invertebrates	1			3.11	**0.002**
Water quality vs. vertebrates	1			1.90	**0.053**
Vegetation vs. invertebrates	1			2.25	**0.024**
Vegetation vs. vertebrates	1			1.83	**0.063**
Invertebrates vs. vertebrates	1			1.11	0.269
Component(Group)	6	0.92	0.97		0.439
Experiment	2	3.53	3.71		**0.031**
Laboratory vs. field	1			2.01	**0.044**
Laboratory vs. natural	1			1.03	0.317
Field vs. natural	1			2.07	**0.040**
Age	1	0.50	0.53		0.463
Residual	196	0.95			

Statistically significant effects ($\alpha = 0.10$, for heuristic purposes and because of unequal sample sizes), including those for *a posteriori* pair-wise comparisons, in bold. # = permutational value (9999 permutations). Notably, no interaction effects are evaluated because of missing cells and highly unequal sample sizes. See also Figure 7D–F.

presence of non-linear relationships between phosphorus and carp biomass (Lougheed et al., 1998), but this was overall in agreement with other studies pointing to contrasting (or no) effects as well as to difficulties in relating carp densities to phosphorus loadings (e.g., Meredith et al., 1995; Roberts et al., 1995). The combined decrease and increase in epiphytic midges reported by Batzer et al. (2000) was instead explained as an interplay between direct and indirect predator-prey effects, whereby indirect suppression of invertebrate competitors and predators on epiphytic midges by carp was more important than their direct predation. Preference by large-bodied, piscivorous waterfowl species for ponds with large carp (as opposed to their avoidance by smaller bird species) was explained in terms of energetic advantages of predation on larger fish prey (Kloskowski et al., 2010). Also, the absence of an effect of carp on fish combined with a negative effect was found to depend on the life stages of the species of centrarchids under study (Wolfe et al., 2009). Finally, the contrasting positive and negative effects on aquatic macrophytes (Hume et al., 1983; Fletcher et al., 1985) and fish (Egerston and Downing, 2004) were most likely the result of the large amount of variability in the natural systems under investigation.

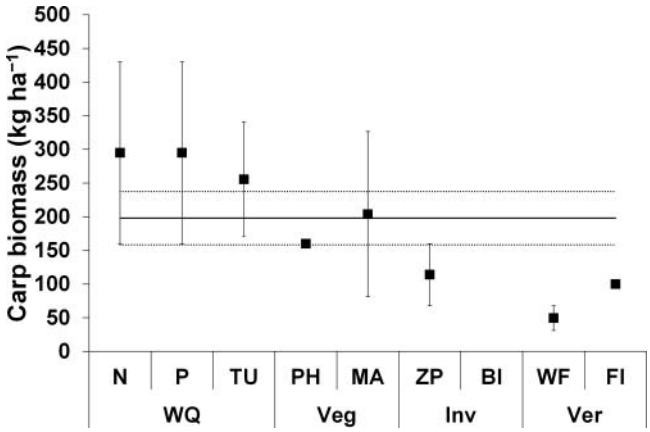

Figure 8 Mean (± SE) biomass threshold for "free-ranging" carp (i.e., based on field experiments using exclosures and natural experiments: Table 5) having an impact on freshwater ecosystems based on components groups and the individual components therein (no data available for amphibians). Overall mean ± SE biomass values (solid and hatched lines, respectively) across all components are also indicated. Abbreviations as per Figure 7.

Strength of Evidence

The causal criteria analysis implemented in the present study has provided consistent, quantitative evidence for detrimental effects (viz., impacts) of carp on freshwater ecosystems, hence supporting previous research based on qualitative, semi-quantitative, or quantitative assessments of representative samples of experiments. This overarching consistency of outcomes was also strengthened by the fact that in no case (i.e., component × experiment combination) was support for the alternative hypothesis provided (Table 9). Thus, impacts were found to occur for all of the ecological components under scrutiny, with the possible exception of zooplankton and waterfowl. However, this was an outcome of inconsistent and insufficient evidence, respectively, resulting from intrinsic difficulties in assessing effects on zooplankton due to the different size and/or functional categories being investigated depending upon study (see Weber and Brown, 2009; Kulhanek et al., 2011) and from the paucity of available experimental, non-management/rehabilitation-oriented studies on waterfowl.

The overall strength of evidence for an impact (i.e., based on all experiments combined) followed a "gradient," with higher values for turbidity/solids, nitrogen, phosphorus, aquatic macrophytes and fish, moderate for phytoplankton/chlorophyll *a* and amphibians, and lower for benthic invertebrates. In this respect, it is remarkable that water quality, aquatic vegetation, and fish were the freshwater ecosystem components originally reported to be negatively affected by carp (Cole, 1905; Cahn, 1929; see *History and Biogeography*, above), and typically flagged as those of higher concern (e.g., Koehn et al., 2000). On the other hand, the moderate strength of evidence for an impact on phytoplankton/chlorophyll *a* was due to the absence of an effect in some experiments, which was attributed in some cases to yet-undefined and complex relationships in aquatic ecosystems (Miller and Crowl, 2006). Finally, in the case of amphibians the overall limited number of experiments is the most likely explanation for the resulting moderate evidence outcome.

The dichotomy in the conclusions from the causal criteria analysis provided by laboratory compared to field and natural experiments, with the former resulting in overall inconsistent evidence and the latter supporting instead the majority of hypotheses, is an indication of the limitations with holding carp within a confined environment; this applied not only to 1+ and older but also to 0+ fish. Conversely, field experiments were able to confirm several of the cause–effect linkages under investigation similar to natural experiments, and with the latter never resulting in inconsistent evidence. This outcome is especially remarkable given the lower number of natural relative to field and laboratory experiments reviewed in this study.

The Conceptual Model Revisited

There was a very close correspondence between the findings of the present study and those by Weber and Brown (2009) as regards the percentage of experiments that reported an increase, decrease or no effect in the ecosystem components under scrutiny. This indicates that the experiments reviewed by Weber and Brown (2009) provided for a representative sample of the entire "population" of experiments that (to the maximum extent possible) was included here. However, whilst Weber and Brown (2009) discussed their proposed middle-out framework in terms of carp effects on shallow-lake (lentic) ecosystems, the current findings indicate that carp may also cause detrimental impacts in lotic habitats (Sidorkewicj et al., 1996, 1998, 1999a, b; Fernández et al., 1998) as well as under extreme water quality conditions (Özbay, 2008). The present review also found impacts to occur under a wide range of climates (sensu Peel et al., 2007), i.e., tropical (e.g. Zambrano et al., 1999), arid (Mazumder et al., 2012), and temperate (e.g. Egerston and Downing, 2004; Rowe, 2007) and cold (Lougheed et al., 1998). This suggests that the detrimental effects of carp may be even wider-ranging than previously thought.

Amphibians and waterfowl were the two additional components that were not originally included in Weber and Brown's (2009) review, and in the present study were found to be impacted upon by carp. In this respect, whilst Weber and Brown's (2009) conceptual diagram included "sportfish biomass" as endpoint node (*sensu* Uusitalo, 2007), the model originally proposed by King (1995) and later refined by Koehn et al. (2000) referred more generically to "other native fauna." In the updated conceptual model proposed in the present study (Figure 6), the latter node could be broken down across three vertebrate components including amphibians, waterfowl, and fish, all of which can be negatively affected by carp. Notably, Koehn et al. (2000) pointed to the need to implement studies to quantify changes that carp are likely to cause to animal communities (including amphibians and birds, and with the exception of the study by Denton and Beebee, 1997), the present review has shown how experimental evidence in regard has since been provided by a total of nine studies (Table 5).

Whilst all pathways in the conceptual models by Koehn et al. (2000) and Weber and Brown (2009) were confirmed by the present findings, the direct impacts on amphibians, waterfowl, and fish as a result of carp foraging and/or spawning behavior were not previously reported. Thus, both 0+ (Hunter et al., 2011) and 1+ carp (Kloskowski, 2011c) were found to prey on tadpoles, even though it remains to be evaluated to what extent this could also have been an artifact of holding carp within a confined space (especially tanks, as in the former experiment). On the other hand, the destruction of nests of the western grebe (*Aechmophorus occidentalis*, Podicipedidae) in vegetated areas of a marsh as a result of spawning activities (La Porte et al., 2014) and the direct predation upon the eggs of white sturgeon (*Acipenser transmontanus*, Acipenseridae) (Miller and Beckman, 1996) were direct effects of carp both documented under natural conditions.

Critical Biomass

Since the findings by Zambrano and Hinojosa (1999), which reported a significant increase in turbidity would already occur at a carp biomass equivalent to 50–75 kg ha^{-1} (L. Zambrano, pers. comm.), field experiments have provided additional evidence for the occurrence of sudden, non-linear shifts from clear- to turbid-water state in shallow water bodies at carp densities of 174–300 kg ha^{-1} (Williams et al., 2002; Parkos et al., 2003; Haas et al., 2007; Matsuzaki et al., 2009a). These results were recently further supported by findings that a threshold carp biomass of $\approx$100 kg ha^{-1} may already cause a dramatic decline in vegetation cover and waterfowl abundance (Bajer et al., 2009), and by laboratory experiments suggesting that not only adults but also 0+ carp can cause dramatic and wide-ranging impacts on freshwater ecosystems, purportedly at biomass values $<$ 175 kg ha^{-1} (Weber and Brown, 2015).

The present study has shown how problematic the provision of a critical biomass value for carp impacts can be if strictly reliant on experimental settings, hence regardless of level of holism. This was demonstrated by the huge range in values resulting from taking all experiments as a whole. These values were the direct outcome of the diverse stocking densities employed, sometimes reflecting traditionally-reported critical biomasses (e.g., Crivelli, 1983; Chumchal and Drenner, 2004; Parkos et al., 2006) or the need to test effects of carp under particularly stressful conditions (Angeler et al., 2002a,b; 2007; Angeler and Rodrigo, 2004). However, even after disregarding the latter type of experiments, there were differences in estimated biomass thresholds both amongst component groups and location of experiments, highlighting the difficulty (if not impossibility) in providing component-wise preset critical values (see below). In fact, incorporation of experiments other than the natural ones into the estimation of critical biomass values inevitably overestimated the latter, suggesting

that future laboratory/field-based experimentation should be more wary in gauging carp stocking densities accordingly, unless there are strong ecological reasons to do otherwise.

Overall, recent experimental evidence of lower critical carp biomass levels than previously thought and the level (198 ± 40 kg ha^{-1}) estimated in the present study may have important implications for the future management of the species in its introduced range. For example, since the surveys by Hume et al. (1983), there has been a tradition in Australia (and New Zealand) to consider a carp biomass > 450 kg ha^{-1} to be critical for detrimental effects on aquatic macrophytes (Fletcher et al., 1985; Osborne et al., 2005; Pinto et al., 2005). Indeed, Australian research on carp has relied on this value, which was based on overseas findings that at such densities carp held in enclosures exerted (or started to exert) the highest impacts on soft-leaved aquatic macrophytes by direct effects (Robel, 1961; Crivelli, 1983), as a reference threshold for the species becoming a pest (cf. Koehn et al., 2000). Laboratory experiments have also relied on this carp stocking density (Hume et al., 1983; Roberts et al., 1995; Khan et al., 2003; Driver et al., 2005). Clearly, this approach needs to be reconsidered in the light of the present findings, and over and beyond the need for support from large-scale natural surveys (see below).

At the same time, the quest for a single, "cast-in-stone" reference value (or range) for critical carp biomass to be employed in further laboratory/field-based experimentation or in gauging the level of carp noxiousness can prove misleading. This was clearly demonstrated by Kulhanek et al. (2011), who developed a predictive (linear) model of increasing severity of impact with increasing carp biomass, which was also a function of preimpact conditions. Within an even broader perspective, this contention is in line with research that highlights the advantages of probabilistic models for the management of water bodies (e.g., Vilizzi et al., 2013b) and with recognition of the unavoidable and all-pervasive relativism whenever tackling invasive fish management issues (Carter, 2009).

Directions for Future Experimentation

As advocated by Carpenter (1999, p. 1086), "[l]arge field experiments, long-term studies and spatially extensive comparisons provide context for microcosm experiments, and sometimes microcosm experiments can contribute to an understanding of larger-scale patterns" (note that, in the present context, "microcosm" equals "laboratory"). Based on the present review, only a fraction of the laboratory-based experimental studies (approximately one third of the total) was carried out in association with a larger field/natural experiment. This was regardless of the often unrealistic constraints imposed by confining carp within enclosures (especially aquaria, tanks, and small artificial ponds), which are likely to limit the validity of experimental findings. An exception to this could be represented by laboratory/field experiments that focused mainly on 0+ fish, as long as the outcomes are eventually interpreted at the appropriate scale (e.g., 0+ carp dynamics, excretion rates) and/or context (e.g., 0+ microhabitat use) (e.g., Weber and Brown, 2015), and with more realistic stocking densities to reflect the more recent findings about lower critical biomass values.

In general, future laboratory- or field-based impact experiments that rely on carp (especially 1+ and older) held within enclosures and/or carried out in isolation are unlikely to advance further our understanding of the processes regulating the network of carp effects on freshwater ecosystems unless they are part of, or related to, larger scale experimental programmes (e.g., Busst and Britton, 2015 vs. Tarkan et al., 2009). Conversely, field-based experiments that are more likely to provide further useful insights into the mechanisms that regulate the eco-engineering effects of carp on freshwater environments are those that rely on: (i) a stocked water body, (ii) exclosures within a water body, or (iii) natural ponds (the three field-based experimental categories identified in the present study lie at the holistic end of the continuum). As mentioned above, such field experiments should ideally be part of long-term and large-scale natural experiments, in accordance with an overall paradigm shift that favors a holistic→reductionist over a reductionist→holistic approach.

Whilst recent research on carp impacts in the United States and Canada has been moving in this direction (e.g., Lougheed et al., 1998; Egerston and Downing, 2004; Bajer et al., 2009; Jackson et al., 2010; Weber and Brown, 2011), it is remarkable that in Australia and New Zealand, the other two high-risk ranked countries in the present study, not much progress has been made in this regard since the first (inconclusive) attempts by Hume et al. (1983) to carry out extensive catchment-level surveys. To this end, Vilizzi et al. (2014a) highlighted the importance of adopting a holistic perspective based on integrated pest management programmes, with possible support from recently developed decision support tools (Vilizzi et al., 2013b). Finally, depending on risk-assessment considerations, there may be a need to implement similar research in all other regions worldwide where carp may represent a threat to freshwater ecosystems. In fact, more extensive field and laboratory will be an essential requirement if informed decisions are to be made for the proper management of carp in its non-native range (Britton et al., 2011b).

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