

# Evaluating and predicting ecosystem services

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## Abstract

The valuation of ecosystem services requires first and foremost, that the current level or stock of a service first be estimated. Here, I investigate the relationship between the fields of environmental science and ecological economics in their research effort of ecosystem services and the implications this may have on the ecosystem valuation research program. I investigate two ecological functions described as ecosystem services within specific ecosystem types: the flood control provisioning services of wetlands and pollination service provisioning by pollinator populations in agroecosystems. I examined the environmental literature to provide quantitative estimates of a) the distribution of the level of service delivered as well as b) the ability of environmental scientists to predict this level of service. The results presented here suggest a moderately strong correlation between research efforts in environmental science and ecological economics at the pooled level of ecosystem types and services. I suggest however, an integrated research enterprise between social and environmental scientists may provide greater efficiency by means of a global ecosystem service research network and repository.

I found that, on average, consistent with conventional wisdom, wetlands do indeed have a positive effect by reducing the frequency and magnitude of floods, increasing low flows, and increasing water storage. In the same vein, I found on average and consistent with conventional wisdom, there is a consistent and comparatively strong association between pollinator abundance and agroecosystem productivity as inferred from measures of plant fertilization success. In both investigations however, metaregression analysis indicated that our current ability to predict either pollination or flood control services is poor to modest at best.

The low predictive power combined with the observed heterogeneity in effect size in both investigations suggest that flood control service delivered by wetlands or pollination services delivered by natural pollinator populations in agroecosystems and the expected changes in the level of services delivered under a candidate management scenario, will have a large uncertainty. Such uncertainty should be explicitly incorporated into estimates

of both the current economic value of ecosystem services, as well as estimates of how these values are likely to change under alternative management scenarios.

Given these, I suggest that the implications for the development of Market-based instruments (MBIs) or any payment of ecosystem services to conserve ecosystem services: that the associated ecological function(s) must be few and well characterized, and we must agree on what endpoints ought to properly be used to characterize these functions. If this condition is not met, an ordinal ranking is the best we can do and in the absence of obvious enthusiasm for more detailed scientific research which leads to the conclusion that perhaps alternate strategies like command and control may be the better alternative to protect ecosystem services.

## *Résumé*

L'évaluation des services de l'écosystème nécessite d'abord que le niveau ou le stock actuel d'un service en particulier soit estimé. J'ai donc étudié la relation qui existe entre le domaine des sciences de l'environnement et de celui de l'économie écologique dans leurs tentatives de recherche des services de l'écosystème ainsi que les implications que cela peut avoir sur le programme de recherche sur l'évaluation des écosystèmes. Pour accomplir ceci, j'ai étudié deux fonctions écologiques décrites comme étant des services de l'écosystème compris dans des types d'écosystèmes particuliers, soit la lutte contre les inondations des services d'approvisionnement des zones humides et l'approvisionnement des services de pollinisation par des organismes animaliers dans les agroécosystèmes. J'ai ainsi étudié la littérature environnemental pour fournir des preuves quantitatives de a) l'estimée de la répartition du niveau des services fournis ainsi que b) la capacité prévisionnelle des spécialistes environnementaux à prédire ce niveau de service.

Les résultats présentés dans cette étude démontrent une corrélation modérément forte entre les efforts de recherche dans les sciences de l'environnement et l'économie écologique au tronc commun des types et des services des écosystèmes. Cependant, au niveau des différents services individuel, la corrélation n'est pas aussi forte, voir-même plutôt faible. Les services recevant le plus d'attention par les scientifiques environnementaux ont plus tendance à être délaissées par les économistes, et vice versa. De plus, j'ai trouvé qu'en moyenne, tel que décrit par la pensée scientifique conventionnelle, les zones humides engendrent un effet positif par l'entremise de la réduction de la fréquence et l'ampleur des inondations, de l'augmentation des courants peu élevés et, finalement, en accroissant le stockage eau. De plus, j'ai trouvé qu'en moyenne et tel que décrit par la pensée scientifique conventionnelle, il y a une relation soutenue et comparativement forte entre l'abondance de pollinisateurs et la productivité des agroécosystèmes tels qu'inférée par les mesures de succès de fécondation de plantes. Cependant, dans les deux enquêtes, une analyse méta-régressive nous indique que notre présente capacité à prédire les services de pollinisation ou de lutte contre les inondations est plus ou moins faible.

Le pouvoir prévisionnelle faible de ces deux enquêtes combiné avec l'hétérogénéité observée dans l'effet de taille laisse entrevoir que le service de contrôle des inondations produit par les zones humides ou les services de pollinisation livrés par des agents animaliers dans les agroécosystèmes ainsi que les changements prévus dans le niveau des services fournis en vertu d'un scénario de gestion de candidat sera doté d'une incertitude accrue. Cette incertitude doit être explicitement intégrée aussi dans les estimations de la valeur économique courante des services de l'écosystème d'autant plus que dans les estimations de la façon dont ces valeurs sont susceptibles de changer sous différents scénarios. Compte tenu de ces résultats, un plan intégré de recherche entre les scientifiques sociaux et environnementaux semble souhaitable. Je crois qu'une plus grande efficacité peut encore toujours être réalisée au moyen d'un réseau de recherche et de référence sur les services de l'écosystème global.

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# **CHAPTER 1. THE RELATIONSHIP BETWEEN ENVIRONMENTAL SCIENCE AND ECOLOGICAL ECONOMICS RESEARCH EFFORT: IMPLICATIONS FOR THE ECOSYSTEM VALUATION RESEARCH PROGRAM**

## **Abstract**

The economic valuation of ecosystem services by economists reflects, in part, the desire to use conventional economic tools (markets and economic instruments) to conserve ecosystem services. However, the estimation of the economic value of ecosystem services requires, first and foremost, that the current level or stock of a service be estimated. This, in principle, is the job of environmental scientists, not economists. Moreover, if the economic valuation of ecosystem services is to be of any practical value in ecosystem management, likely changes in service delivery must be estimated under alternative management scenarios. Again, this is the domain of environmental scientists, not economists. These considerations suggest an effective and efficient research agenda - at least from the perspective of ecosystem management on the ground/in the water - requires that (a) economists focus on ecosystems and their associated services for which the current scientific knowledge permits some level of prediction; and (b) environmental scientists focus on ecosystems and their associated services for which economic valuation tools exist and can be applied. Here I provide a quantitative assessment of the relationship between the effort expended by environmental scientists and ecological economists on different ecosystem types and services using hits in bibliographic databases as a measure of research effort. I find that there is a positive, moderately strong correlation between research efforts in the two domains, a result that, while encouraging, is likely to reflect serendipity rather than the deliberate design of integrated environmental science-environmental economics research programs on ecosystem services. I suggest ways and means by which a tighter, more integrated research program between environmental scientists and environmental economists might be affected.

## Introduction

The idea that ecosystems provide services contributing to human welfare was introduced in 1977 when Walter E. Westman defined 'Nature's Services' as the social value of the benefits ecosystems provide, values that should be estimated such that society can make more informed policy and management decisions (Westman 1977). Subsequently, Paul and Anne Ehrlich defined 'ecosystem services' as "the dependence of human civilization on the services provided by natural ecosystems" (Ehrlich & Ehrlich 1981). Since then, the term has been used to characterize a rather broad range of the benefits that humans derive through the conditions and processes of natural ecosystems.

Perhaps inevitably, just what does or does not constitute an ecosystem service is, to some degree, a matter of taste. But generally speaking, ecosystem (or ecological) services (Table 1.1) can be regarded as classes of *ecosystem functions* that (1) demonstrably contribute to human welfare; and (b) can be assigned a unit (or other) utility (Costanza et al. 1997). Services provided by ecosystems are valued in some sense but, at least hitherto, have only rarely had associated markets. Moreover, ecological services are also characterized by their non-exclusive ownership. By contrast, ecological *goods* are considered to be the products (e.g., medicinal plants, timber, and other raw materials) of ecological processes that have economic value and for which a market exists (Fisher et al. 2009). Because services are classes of ecological functions, some services (e.g. pollination) subsume only a single ecological function, other services (e.g. water regulation) multiple functions (Table 1.1).

### ***The state of the world's ecosystem services***

The Millennium Ecosystem Assessment (2005a) notes that over the past 50 years, humans have changed ecosystems more than any other comparable time in human history. These changes reflect largely an increasing demand for food, fresh water and raw materials. Of perhaps even greater concern, 15 of 24 ecosystem services were considered to be in a state of decline, reflecting, in large part, anthropogenic degradation. The report notes that

degradation of ecosystem services could grow substantially worse in the first half of the 21<sup>st</sup> century and reversing this degradation will only be possible if significant changes in policy and practices are adopted. Most distressingly, there is evidence that human impacts on ecosystem services may be non-linear (Groffman et al. 2006, terHorst and Munguia 2008, Cortina et al. 2006, Kools et al. 2009) leading to the potential for large-scale, irreversible changes such as abrupt changes in water quality, creation of dead zones in coastal waters, collapse of fisheries, and shifts in regional climate.

The potential consequences of the global decline in ecosystem services are enormous. For example, declining per capita availability of water has resulted in demonstrable negative impacts on human welfare and water scarcity affects some 1-2 billion people worldwide, with inadequate water sanitation causing some 56 million deaths annually (Millennium Ecosystem Assessment 2005a). Developing nations are the most vulnerable to changes in hydrological services leading to increased prevalence of water-related diseases such as diarrhoea and schistosomiasis because they lack alternatives (Pattanayk & Wendland 2007), and when alternatives do exist, replacement costs for hydrological services can be well over US\$20 million (McClennan 2007). Degradation of vegetated coastal ecosystems has been estimated to significantly increase release of carbon dioxide resulting in economic damages of \$US 6-42 billion annually (Pendleton et al. 2012). Degradation of wetlands and high-cover grassland in response to land use changes caused by climate change and human activities in Zoige Plateau, China has resulted in an estimated decline in the value of ecosystem services from  $61.46 \times 10^9$  yuan (approx. \$US 9.97 billion) in 1975 to  $58.61 \times 10^9$  yuan (approx. \$US 9.5 billion) in 2005 (Li et al. 2010).

### ***Economic Valuation of Ecosystem Services***

If ecosystem services contribute to human welfare, they have value. In principle at least, some of this value may be economic. Insofar as many decisions concerning ecosystem management are made on the basis of (real or imagined) economic value, the possibility exists of using standard economic tools (markets and economic instruments) to conserve ecosystem services. So for example, if the economic value of a wetland as a source of groundwater recharge, flood control, and surface water filtration is sufficiently large, then

(so the argument goes), there may be a *bona fide* economic incentive to maintaining natural wetlands as opposed to draining them for residential or commercial development.

There is, therefore, considerable attraction (especially for economists) in using the economic valuation of ecosystem services as a rationale for ecosystem conservation. A simple bibliographic search retrieved 613 studies published since 1991 concerned with ecosystem valuation at local to global scales. The early bar height was set by Robert Costanza and colleagues who used seventeen of the basic ecosystem services from 16 biomes to estimate the global value of these services at \$US 33 (16-54) trillion each year (Costanza et al. 1997). Although several global assessments exist (Costanza et al. 1997, O'Higgins et al. 2010), ecosystem valuation studies have more commonly been undertaken at local and regional scales (Dong et al. 2007, Naidoo et al. 2009).

Although economic valuation methods can be employed to estimate the economic value of a suitably defined unit of ecological service (Solberg 1997, Xiao et al. 2005), estimating the economic value of a service delivered by an entire ecosystem (as has been attempted, for example, by e.g. Adger et al. 1995, Barbier 1994, Loomis et al. 2000) requires that the current level of the service in question be estimated. This, in principle, is the job of environmental scientists, not economists. Because ecosystem services derive from ecosystem functions, from the perspective of environmental scientists, the problem reduces to one of estimating the level of a particular function in the ecosystem of interest. Thus, if the economic evaluation of ecosystem services is to inform ecosystem management on the ground/in the water, we need to know with what accuracy and precision we can estimate:

- (1) the level or amount of a particular function sustained by an ecosystem in its current state; and
- (2) the level or amount of the function sustained by an ecosystem under alternate management regimes and/or states.

The importance attached to this question by environmental scientists is itself telling. In a recent survey of 34 Canadian environmental scientists who were asked to identify existing

knowledge gaps impeding effective ecosystem management (Rudd et al. 2010), the top identified question (of 396 submitted) was: “To what extent can ecological function and the supply of ecosystem services be predicted on the basis of ecosystem composition and structure?” Our ability to predict the level of services provided by an ecosystem is positively related to our knowledge of the system in question: the more knowledge, the greater the predictive power – indeed, for many scientists predictability is the litmus test of (true) knowledge (Sarewitz 2000, Miller et al. 2004). And, one presumes, the more effort devoted to accruing knowledge, the more knowledge so accrued – although the relationship need not be linear.

From the perspective of informing ecosystem management, having a method of evaluating the economic value of the ecosystem services is of little practical value in the absence of an empirical estimate of the level of services currently provided, and the expected level under different management regimes. Similarly, being able to estimate – even if accurately and precisely – the level of services provided is of considerably less value to the decision-making process in the absence of a legitimate method of estimating their associated economic value. It follows, then, that an efficient research agenda (from the perspective of ecosystem management on the ground/in the water) requires that (a) economists should focus on ecosystems and their associated services for which current scientific knowledge permits some level of prediction about the level of such services, both currently and under alternative management regimes; and (b) environmental scientists should make some attempt to focus their research activities on ecosystems and their associated services for which economic valuation tools exist and can be applied.

The question is: do they? Here I answer this question by considering the relationship between the research effort expended by environmental scientists and ecological economists on different ecosystem types and services, where research effort is quantified by the number of peer –reviewed publications (hits) in a set of bibliographic databases.

## **Methods**

An Environmental Science-Economic-Ecosystem Services (EEES) database was created by constructing a set of defined search strings for various ecosystem services associated with a particular ecosystem type. The resulting database includes: (1) the target ecosystem service and associated search terms (Table 1.2); (2) a broad ecosystem type designation; (3) a more refined ecosystem type designation; and (4) the number of hits associated with a specific combination of service and broad/refined ecosystem type obtained by searching a specific bibliographic database.

### ***Bibliographic databases***

Bibliographic databases included Academic Citation Indices-Thompson Reuter's ISI Web of Knowledge and ISI Web of Science, Elsevier's SciVerse Scopus and the academic database-EBSCOhost. During preliminary research Environmental Reference Valuation Inventory (EVRI) -an Environment Canada run "searchable storehouse of empirical studies on the economic value of environmental benefits and human health effects" (EVRI 2012) was used as a candidate database but was abandoned after further analysis, as it was clear the database was outdated (e.g. only 16 records between 2012-2013, while Web of Knowledge produced 503 and Scopus, 968).

A recent review of ecological literature databases found Web of Science and Scopus to be two of the best databases for finding primary ecological literature based on 1,010 citations (Brown 2007). All databases used in this study have the 20 top-ranked ecology journals included in their catalogs (Brown 2007).

### ***Ecosystem services***

I began with an initial set of 17 services based on the Costanza et al. (1997) and De Groot et al. (2002) taxonomy (Figure 1.1). Of these, 12 were eliminated simply because the set of ecological functions which in principle could affect the level of such service was deemed too large and diffuse. For example, the set of functions which in principle could

affect the degree to which ecosystems provide refugia, raw materials and genetic resources was considered both comparatively large and comparatively ill-defined.

### ***Ecosystem types***

I adopted an ecosystem classification system very similar to that of the Millennium Ecosystem Assessment (2005a). Ecosystem types included: Forest (Boreal, Temperate, Tropical), Dryland (Temperate grassland, Mediterranean, Tropical Grassland and Savanna, Desert), Inland Water, Coastal, Marine, Island, Mountain, Polar. The generic inland water class was replaced with three more refined ecosystem types (lakes, bays and ponds). More refined ecosystem sub-types were defined based on the World Wildlife Fund classification scheme (Abell et al. 2008, Spalding et al. 2007, Olson et al. 2001) to create 11 broad ecosystem classes and 49 subclasses (Appendix A).

### ***Environmental science research effort***

For ISI Web of Science I retrieved articles associated with a given combination of search terms. All searches included two fields:

- |      |  |
|------|--|
| (i)  | FIELD 1: “ecosystem service” OR associated synonyms. |
| (ii) | FIELD 2: (broad or refined) “ecosystem type”.        |

For example, a search to retrieve studies concerned with the ‘erosion control’ services provided by coastal ecosystems would have:

FIELD 1: “erosion control” OR “soil conservation” OR “sediment retention” OR “soil retention” OR “sediment capture” OR “erosion regulation” OR “erosion mitigation” OR “sediment control” OR “soil stability”

AND

FIELD 2: “coastal”

Searches were done with lemmatization off (thus, only the original term was

queried, not inflected forms such as plurals or synonyms), but in instances where an ecosystem type might be referred to in the plural or with alternate endings (i.e. grassland or grasslands) the \*asterisk symbol was used. Some ecosystem types required the use of more than one entry per field. For example Temperate Forest/Woodlands required a search that included: "forest\*" OR "woodland\*" AND "temperate".

All citations retrieved using a particular search string (that is, combination of ecosystem type and ecosystem service synonyms) were considered a hit. As there are 60 (11 broad ecosystem classes and 49 subclasses) ecosystem types and 5 ecosystem services, there are  $N = 300$  combinations in total, with a given database yielding a count (number of hits) for each combination.

Because specific hits could appear in multiple databases, I kept track of all hits and removed any duplicates that arose either from (a) occurrences in multiple databases; or (b) multiple retrievals from the same database in response to different search strings (e.g. different ecosystem service synonyms.).

### ***Economic valuation research effort***

The procedure was the same as that employed to quantify environmental science research effort in ISI Web of Science with one difference: for each economic proxy bibliographic databases (ISI Web of Knowledge, Scopus and EBSCOHost), all searches included:

Field 1 (topic): "ecosystem service" OR associated synonyms...

Field 2 (topic): (broad or refined) "ecosystem type"

Field 3 (topic): valuation OR valuing OR "willingness to pay" OR contingent OR hedonic OR "economic valu\*" OR "willing to pay" OR "revealed preference" OR "stated preference" OR "replacement cost" OR "travel cost" OR "damage cost avoided" OR "damages avoided".

## Results

There was a moderate to strong correlation (0.64-0.84) between research effort in the two domains for a given ecosystem service (Table 1.3), which translates into a moderate overall correlation when pooling over services (Figure 1.2). On average, for a given ecological service, research effort in the environmental sciences was dramatically greater than in ecological economics (Figure 1.3). When individual ecosystem services are examined it is apparent that those services of most interest to environmental scientists (as measured by citations) are not necessarily of most interest to economists-see example, pollination and vice versa-see example, flood control (Figure 1.3). This result is comparatively robust: over the 56 ecosystem types (irrespective of ecosystem services and associated functions), database counts were highly correlated (range 0.78-0.92) (Table 1.4, Figure 1.4) between the two domains. Four ecosystem types were removed from this log10 ecosystem type analysis for not having enough information across databases.

Using the same search methodology I created citation reports to examine if there was a difference in citation rates between ecological economics and environmental science. For ecological economics: average citations per item=15.46 (N=2022). For environmental science: average citations per item=14.87 (N=6580).

## Discussion

My review of the environmental science literature on ecosystem functions, and the economic literature on the valuation of corresponding ecosystem services, suggests a moderately strong correlation between research efforts in the two domains for a given ecological service. The implication is that, for a given service, those ecosystem functions and or ecosystem types receiving attention by environmental scientists tend also to be those receiving attention by economists, and *vice versa*. If greater research effort (as estimated by number of hits in literature searches) implies greater knowledge, and greater knowledge implies greater predictability, my results suggest that economists are tending to focus their efforts on the ecosystems and services for which there is likely to be a greater ability to predict current levels of a given service and, possibly, how such levels might be expected to change under different management scenarios.

The estimated correlation between research effort in the two domains for a given ecosystem service is surprisingly strong, given the potential sources of error. Various factors might be expected to reduce the observed correlation between the efforts expended by environmental scientists in gaining greater knowledge and predicting the level of services delivered by an ecosystem, and the efforts of economists to gain greater knowledge on how such services are valued. One obvious source of error is the difficulty in completely and comprehensively characterizing a specific ecosystem service with respect to a defined set of search synonyms. If the probability of retrieving a relevant article, given a particular synonym (search phrase), differs between the two domains, this will, in effect, increase measurement error, thereby reducing the observed correlation.

Another potential source of error is the different focal points of the two research domains. The relationship between human activities and ecosystem functions is – properly - the focus of attention for environmental scientists, and the valuation of ecosystem services is - properly - the focus of social scientists and economists. And this focal difference is not just applicable to economists: rarely are respondents in, for example, stated preference approaches, sufficiently knowledgeable about ecosystem functions to be able to ascribe value to them (Barkmann et al. 2007). Rather, they ascribe value to goods and/or services,

both of which may be sustained by a number of different ecosystem functions. In the current analysis, differences between the two domains of inquiry with respect to the characterization of particular services, and their association functions, will again increase measurement error, thereby reducing the observed correlation.

The ecosystem service approach, as originally proposed (Costanza and Daly 1992, Perrings et al. 1992, Costanza et al. 1997), offers some promise of preserving the planet's increasingly diminished natural capital. As Daily et al (2009) note, this requires translating knowledge about ecosystem services into effective and efficient policy and decision-making tools. The problem, however, is not simply that ecosystem services are undervalued (Costanza et al. 1997, Postel and Thompson 2005), but that they are poorly characterized and poorly understood scientifically (Kremen 2005, Chan et al. 2006, Wallace 2007). In Daily et al.'s words, "In promising a return (of services) on investments in nature, the scientific community needs to deliver the knowledge and tools necessary to forecast and quantify this return" (Daily et al. 2009). If the promise of the ecosystem services approach is to be fulfilled, environmental science must develop and deploy the tools necessary to predict the impact of human activities on ecosystem functions and the services they support: the role of the social sciences is to measure the values ascribed to these services by people.

While it is still comparatively early in ecosystem service work I assert for a centralized plan on ecosystem services which would yield a flow of benefits from a complementarity of focus. If economists and environmental scientists don't study ecosystem and (their services) in similar proportions the whole ecosystem service research program because flawed. For this program to work efficiently and effectively we need: (1) an economic methodological framework capable of attributing value to ecosystem services and (2) for policy and management implication-the ability to estimate the level of service being delivered and the ability to predict the changes in this level with different management actions/decisions. Addressing current gaps and opportunities would drive towards a more efficient research agenda by greater centralization. Current approaches to conservation and natural-resource management often focus on single objectives, resulting in many unintended consequences.

Given the above, an integrated research enterprise between social and environmental scientists seems desirable (Carpenter et al. 2009, Chazdon et al. 2009) and, indeed, in the context of several specific ecosystems and services, has already been deployed (e.g. Daily et al. 2009, Raymond et al. 2009, Tallis and Polasky 2009). The value of interdisciplinary research networks to gain insight into the components of ecosystems and the services they provide is being increasingly recognized (Mangi et al. 2010, Mace et al. 2012). While my results indicate that, at least at a coarse level, environmental scientists and ecological economists may at least be pulling in the same direction, I believe that greater efficiency may yet still be achieved by means of a global ecosystem service research network and repository. Such a repository would explicitly link research in the biophysical sciences on the measurement and prediction of ecosystem functions with that of the social sciences on the valuation of ecological services via three separate link attributes: (a) geospatial and temporal location; (b) ecosystem type(s) and; (c) ecosystem services and associated ecosystem functions. Such a repository would also permit researchers in the biophysical sciences to link directly with researchers interested in the development and application of methods to estimate the economic value of such services. Moreover, such a network would, at least in principle, facilitate a more efficient research agenda whereby (a) economists focus on ecosystems and their associated services for which the current scientific knowledge permits some level of prediction about, minimally, current service levels; and (b) environmental scientists focus on ecosystems and their associated services for which validated economic valuation tools exist and can be deployed.

## Tables

Table 1.1. Ecosystem services, associated ecosystem function classes and processes

(Adapted from De Groot et al. 2002).

| <b>Ecosystem Service</b>               | <b>Ecosystem processes/components</b>  |
|--|--|
| <i>Regulation functions</i>            | Maintenance of essential ecological processes and life support systems                                 |
| 1. Gas regulation                      | Role of ecosystems in bio-geochemical cycles   |
| 2. Climate Regulation                  | Influence of land cover and biol. mediated processes on climate  |
| 3. Disturbance prevention              | Influence of ecosystem structure on dampening environmental disturbances                               |
| 4. Water regulation                    | Role of land cover in regulating runoff & river discharge  |
| 5. Water supply                        | Filtering, retention and storage of fresh water  |
| 6. Soil retention                      | Role of vegetation root matrix and soil biota in soil retention  |
| 7. Soil formation                      | Weathering of rock, accumulation of organic matter   |
| 8. Nutrient regulation                 | Role of biota in storage and re-cycling of nutrients   |
| 9. Waste treatment                     | Role of vegetation & biota in removal or breakdown of xeric nutrients and compounds                    |
| 10. Pollination                        | Role of biota in movement of floral gametes  |
| 11. Biological control                 | Population control through trophic-dynamic relations   |
| <i>Habitat functions</i>               | Providing habitat (suitable living space) for wild plant and animal species                            |
| 12. Refugium function                  | Suitable living space for wild plants and animals  |
| 13. Nursery function                   | Suitable reproduction habitat  |
| <i>Production Functions</i>            | Provision of natural resources   |
| 14. Food                               | Conversion of solar energy into edible plants and animals  |
| 15. Raw materials                      | Conversion of solar energy into biomass for human construction and other uses                          |
| 16. Genetic resources                  | Genetic material and evolution in wild plants and animals  |
| 17. Medicinal resources                | Variety in (bio)chemical substances in, and other medicinal uses                                       |
| 18. Ornamental resources               | Variety of biota in natural ecosystems with (potential) ornamental use                                 |
| <i>Information Functions</i>           | Providing opportunities for cognitive development  |
| 19. Aesthetic information              | Attractive landscape features  |
| 20. Recreation                         | Variety in landscapes with (potential) recreational Travel to natural ecosystems for eco-tourism, uses |
| 21. Cultural and artistic information  | Variety in natural features with cultural and artistic value   |
| 22. Spiritual and historic information | Variety in natural features with spiritual and historic value  |
| 23. Science and education              | Variety in nature with scientific and educational value  |

Table 1.2. Ecosystem functions and corresponding synonyms that were used in searches. (<sup>a</sup> used in preliminary analysis only).

| Ecosystem Services      | Flood Control            | Erosion Control           | Carbon Sequestration       | Pollination            | Soil Formation         | Nutrient Cycling <sup>a</sup> | Biological Control <sup>a</sup> |
|-------------------------|--------------------------|---------------------------|----------------------------|------------------------|------------------------|-------------------------------|---------------------------------|
| Alternate Search Phrase | <i>Flood Prevention</i>  | <i>Soil Conservation</i>  | <i>Carbon Capture</i>      | <i>Seed Production</i> | <i>Pedogenesis</i>     | <i>Nutrient Balance</i>       | <i>Pest Control</i>             |
|                         | <i>Flood Attenuation</i> | <i>Sediment Retention</i> | <i>Carbon Uptake</i>       | <i>Seed Dispersal</i>  | <i>Soil Conversion</i> | <i>Nutrient Regulation</i>    | <i>Pest Regulation</i>          |
|                         | <i>Flood Regulation</i>  | <i>Soil Retention</i>     | <i>Sequest* Carbon</i>     | <i>Seed Movement</i>   | <i>Soil Generation</i> | <i>Nutrient Distribution</i>  | <i>Disease Control</i>          |
|                         | <i>Storm Protection</i>  | <i>Sediment Capture</i>   | <i>Carbon Accumulation</i> |                        | <i>Soil Fertility</i>  | <i>Nitrogen Fixation</i>      | <i>Disease Regulation</i>       |
|                         | <i>Flood Mitigation</i>  | <i>Erosion Regulation</i> | <i>Carbon Fixation</i>     |                        | <i>Peat Formation</i>  | <i>Phosphorus Cycle</i>       | <i>Population Control</i>       |
|                         | <i>Flood Protection</i>  | <i>Erosion Mitigation</i> |                            |                        |                        | <i>Sulfur (sulphur) Cycle</i> |                                 |
|                         |                          |                           | <i>Sediment Control</i>    |                        |                        | <i>Nitrogen Cycle</i>         |                                 |
|                         |                          | <i>Soil Stability</i>     |                            |                        |                        |                               |                                 |
|                         |                          | <i>Erosion Prevention</i> |                            |                        |                        |                               |                                 |

Table 1.3 The correlation between environmental science and economic valuation research effort for 5 ecosystem services based on different bibliographic database searches for a defined set of N=60 ecosystem types. Results were Log<sub>10</sub> transformed.

| ISI Web of Science   | ISI Web of Knowledge | Scopus | EBSCOHost |
|----------------------|----------------------|--------|-----------|
| Flood Control        | 0.74                 | 0.80   | 0.84      |
| Carbon Sequestration | 0.71                 | 0.70   | 0.81      |
| Erosion Control      | 0.75                 | 0.76   | 0.57      |
| Soil Formation       | 0.60                 | 0.78   | 0.71      |
| Pollination          | 0.62                 | 0.75   | 0.63      |

Table 1.4. The Log<sub>10</sub> correlation coefficients between measures of ecosystem type (n=56) research effort in five different bibliographic databases.

|  | <i>Log<sub>10</sub> ISI<br/>Web of<br/>Science</i> | <i>Log<sub>10</sub><br/>EVRI</i> | <i>Log<sub>10</sub> Web<br/>of<br/>Knowledge</i> | <i>Log<sub>10</sub><br/>Scopus</i> | <i>Log<sub>10</sub><br/>EBSCOHost</i> |
|--|--|----------------------------------|--|------------------------------------|---------------------------------------|
| <i>Log<sub>10</sub> ISI Web of<br/>Science</i> | 1  |                                  |  |                                    |                                       |
| <i>Log<sub>10</sub> EVRI</i>                   | 0.78   | 1                                |  |                                    |                                       |
| <i>Log<sub>10</sub> Web of<br/>Knowledge</i>   | 0.92   | 0.83                             | 1  |                                    |                                       |
| <i>Log<sub>10</sub> Scopus</i>                 | 0.92   | 0.83                             | 1  | 1                                  |                                       |
| <i>Log<sub>10</sub> EBSCOHost</i>              | 0.91   | 0.84                             | 0.92   | 0.92                               | 1                                     |

## Figures

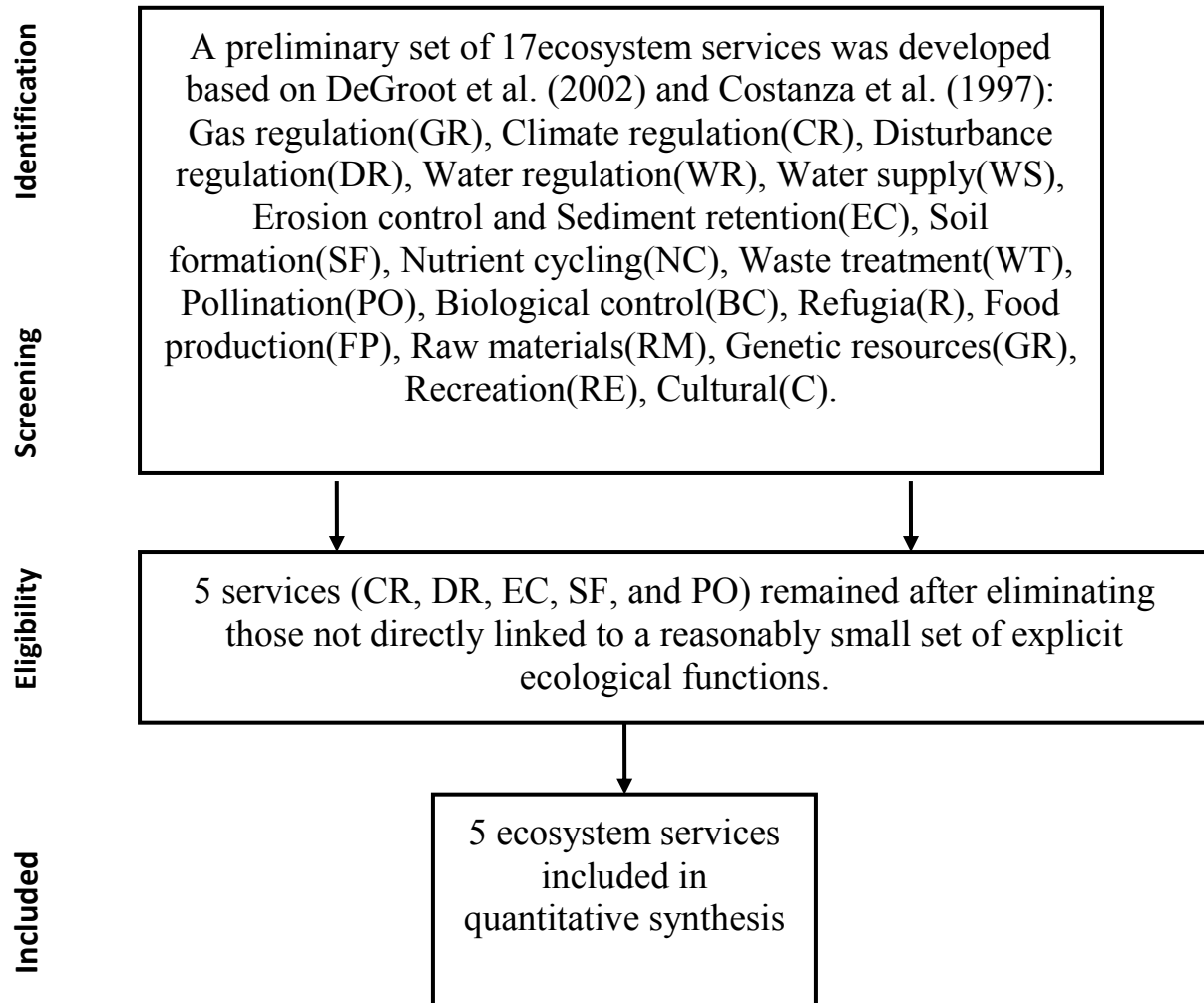


Figure 2.1. Flow diagram for selection of ecosystem services included in the analysis of the relationship between research effort in environmental science and environmental economics.

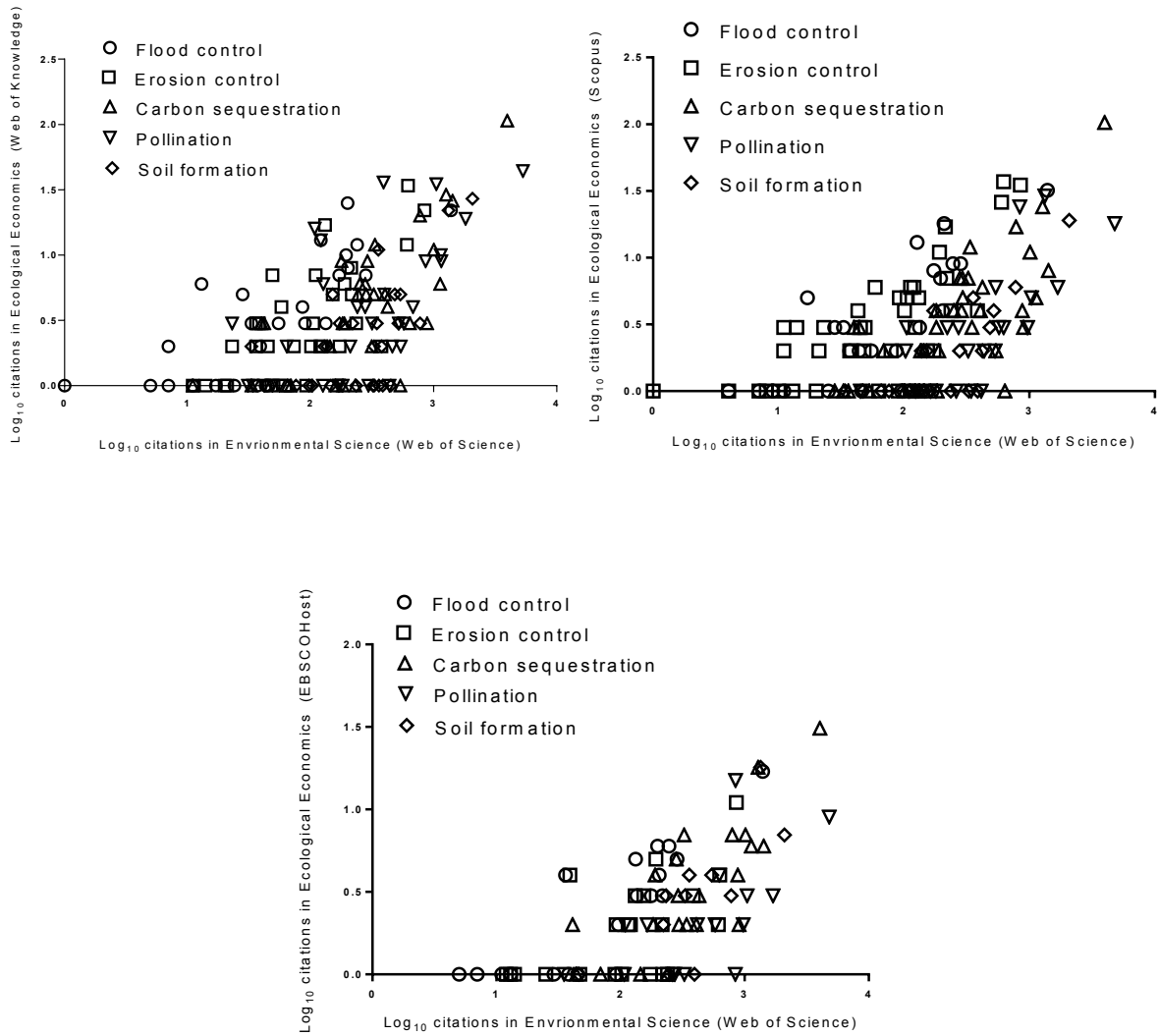


Figure 1.2. The correlation between research effort ( $\log_{10}$ ) retrieved citations or “hits” in ecological economics and environmental science based on several different bibliographic databases. Each datum in the figure represents a given ecosystem service and ecosystem type.

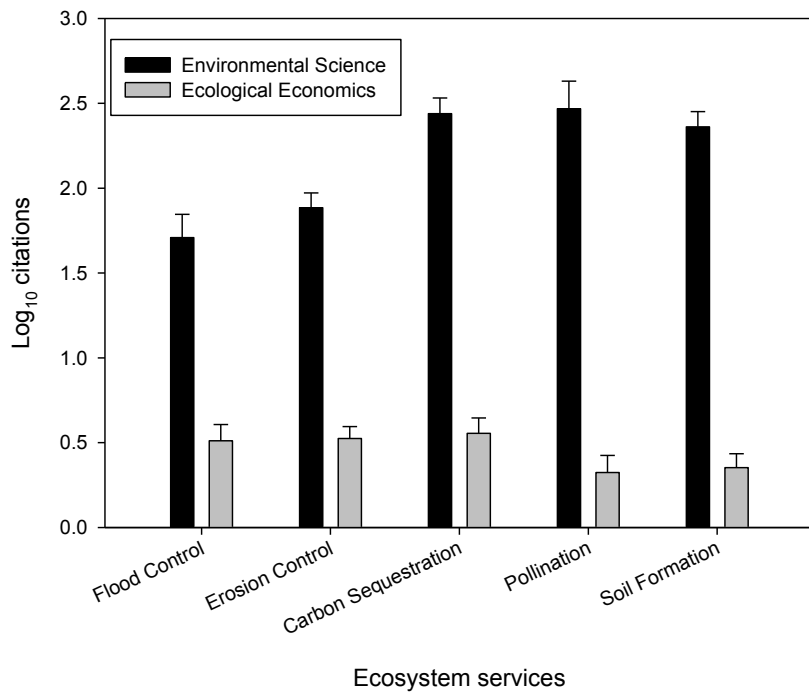


Figure 1.3. Average environmental science (ISI Web of Science) and ecological economics research effort (Web of Knowledge, Scopus) log<sub>10</sub> citations for five selected ecosystem services across 60 ecosystem types. Averages and associated standard errors are based on number of citations (hits) in databases used to measure environmental science and ecological economic literature.

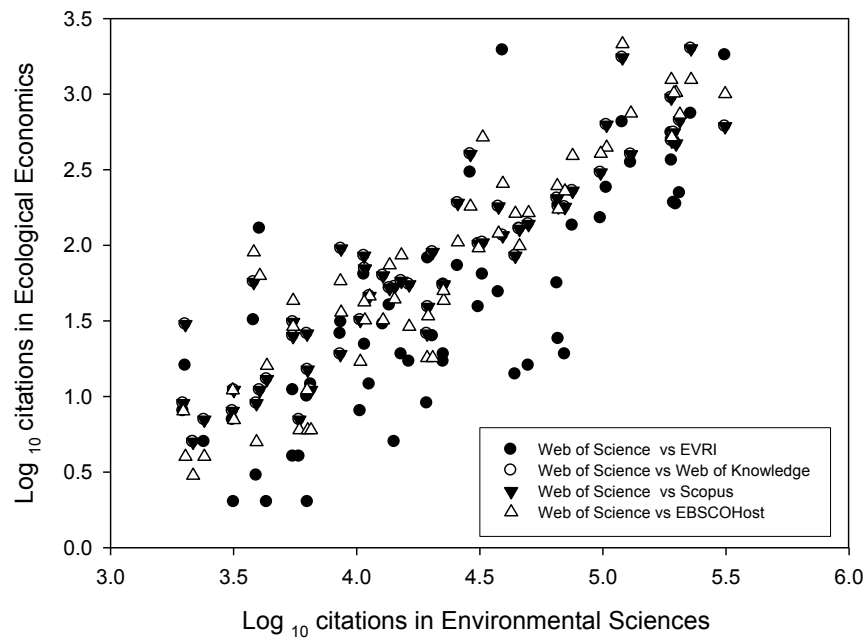


Figure 1.4. The correlation between research effort ( $\text{log}_{10}$ ) retrieved citations or “hits” in environmental sciences (ISI Web of Science) and ecological economics (EVRI, Web of Knowledge, Scopus and EBSCOHost) databases for 56 different ecosystem types.

## **CHAPTER 2. FLOOD CONTROL PROVISIONING SERVICES OF WETLANDS**

### **Abstract**

Wetlands are unique ecosystems that provide a range of services, including ground water recharge, nutrient retention, waste assimilation, shoreline stabilization, and carbon storage. One of the most cited and economically valued services provided by wetlands is flood control, that is, the ability of these ecosystems to mitigate flooding. With wetland ecosystems disappearing in the developed world due to drainage for cultivation, deforestation and flow and flood control-levees and dams, there is mounting concern over the resulting loss in natural flood control services and the associated economic values. Here I employed a meta-analysis of the primary literature to determine the extent to which environmental scientists can estimate the level of flood control services provided by wetlands in their current state, and how this level will change in response to changes in ecosystem state arising from different management regimes or decisions. I found that, on average, consistent with conventional wisdom, wetlands do indeed have a positive effect by reducing the frequency and magnitude of floods, increasing low flows, and increasing water storage. Nonetheless, my results also indicate that the ability to predict the level of ecological service provided by wetlands, based on information about potential predictors, is modest at best. This, combined with the observed heterogeneity in effect sizes means that there will be generally large uncertainty associated with estimates of the current level of flood control service delivered by a wetland, or the expected change in the level of service delivered under a candidate management scenario.

## Introduction

The Millennium Ecosystem Assessment has provided a comparatively recent evaluation of the current state of the world's ecosystems and the services they provide. The news is not good: of 24 identified services, 62.5% are considered to be in serious decline (Millennium Ecosystem Assessment 2005a). Of particular concern is the deteriorating state of the world's wetlands, and associated declines in the ecological services wetlands provide. More than 50% of certain types of wetland have disappeared in parts of North America, Europe, Australia, and New Zealand during the twentieth century (Millennium Ecosystem Assessment 2005b) (For North America, the estimates refer to inland water and coastal marshes and emergent estuarine wetlands; the estimates for Europe include the loss of peatlands; those for Northern Australia are for freshwater marshes, while estimates for New Zealand are of inland and coastal marshes.)

Loss of natural flood control services due to wetland degradation has been linked to a wide range of anthropogenic activities, including drainage for cultivation (Zedler 2003), deforestation (Komatsu et al. 2011), flow and flood control-levees and dams (Kingsford 2000), and to a lesser extent, species invasion (Mitchell et al. 2011) and pollution (Carpenter et al. 1999). Continued drainage of riverine floodplains globally is expected to lead to dramatic reductions in ecosystem services within the next few decades (Tockner and Stanford 2002). Wetland drainage (estimated 3,600 cubic kilometres a year from inland wetlands), and pollution (inorganic nitrogen in wetlands doubled and in some industrialized areas has increased more than tenfold the global amount in 1960) has put the people who depend on them and their services at risk (Millennium Ecosystem Assessment 2005b) (Bedford and Preston 1988). For example, modification of African wetlands led to a reduction in the value of provided goods and services, with the burden of the reduced services being borne by local communities (Schuyt 2005).

Ground water recharge, nutrient retention and cycling, waste assimilation, water purification, shoreline stabilization, and evapotranspiration are all services that wetlands are considered to provide, at least in principle (Brauman et al. 2007; Mitsch and Gosselink

2007, p.347-355). But arguably the most cited service is flood control. Because of their low topographic position relative to uplands (e.g. isolated depressions, floodplains), wetlands store surface water, rain, snowmelt, groundwater and flood waters, thereby attenuating peaking events to a slower release of discharges over long periods of time (Mitsch and Gosselink 2007, p.347). There is evidence that floodplain wetlands reduce the frequency (Acreman et al. 2003, Hillman 1998), magnitude (Ogawa et al. 1986, Ferrari et al. 1999) or timing (Hardy et al. 2000, Walton et al. 1996) of flood events. Similar results have been obtained for headwater wetlands (e.g. Nicholson et al. 1989, Wu and Johnston 2008). Draining wetlands in New Zealand was shown to increase the frequency of flood peaks greatly  $> 10 \text{ l s}^{-1} \text{ ha}^{-1}$  (Jackson 1987). A case study of wetlands in Illinois estimated that as the peakflow to average precipitation ratio decreased by (on average) 3.7 percent, floodflow volume to total precipitation ratio decreased by 1.4 percent, and low flow increased by 7.9 percent for an increase of one percent wetland area in a watershed (Demissie and Khan 1993). Even beaver dams can substantially reduce discharge peaks downstream (Nyssen et al. 2011)

But there is also evidence that wetlands can, under certain conditions, increase flood peaks (Bullock and Acreman 2003). Although many researchers contend that wetlands have a mitigating influence on flood volume, others are of the view that wetland drainage has no impact on flooding (e.g. Bengston and Padmanabhan 1999). Hence, it is unclear to what extent floods of different magnitude are attenuated (or enhanced) by wetlands of different types and sizes located in different geographic regions (Cernohous 1979, Smakhtin and Batchelor 2005). Although many published statements exist on the impact of headwater wetlands or floodplain wetlands on parameters related to floods (Bullock and Acreman 2003), few quantitative estimates exist.

The flood control services sustained by wetlands have also been of interest to economists (Gren et al. 1995, Mitsch and Gosselink 2000) because of the health and safety hazards posed by floods (Reed and Field 1992, Lehner et al. 2005) and the attendant direct financial implications of loss of life and property and subsequent longer-term socioeconomic consequences (Ginexi et al. 2000). Estimates of the economic value of flood

control services range from US (1990) \$89 to \$1747 per acre of single-service wetlands (Woodward and Wui 2001). The true costs of floods are, moreover, likely to increase in the future, as there is ample evidence that, in many parts of the world, the frequency and magnitude of flood events is expected to increase under most climate change scenarios (Milly et al. 2002, Nicholls 2004). Flood frequencies have increased significantly on all continents over the past 60 years, with flood events occurring 3 to 6 times more frequently than in 1950 (Millennium Ecosystem Assessment 2005a).

The potential economic consequences of floods have led institutions responsible for wetland management to consider more seriously the consequences of loss or degradation of wetland habitat (EPA 2006, OMNR 2011). These deliberations have, in some circumstances at least, contributed to the implementation of wetland protection measures. For example, the Jiuduansha Shoals Wetland involved the setting aside of 420 square kilometers as a Nature Reserve by the Chinese government along the Yangtze River (Jin 2010) to protect the valuable ecosystem services (e.g. land forming, material production, air conditioning, water impoundment and purification) provided by the estuarine wetland. In New Orleans, Louisiana coastal wetlands were conserved and restored to a level exceeding the no net loss policy recommended in the State's Wetlands Conservation Plan (State of Louisiana 1997), adopted in 1997. Additional measures included establishing a land use category for natural isolated wetlands and prohibiting wetland drainage both inside and outside the levees (New Orleans Master Plan 7.13, 7.14. 2010). As yet another example, as an alternative to building much more costly flood control structures to reduce downstream flooding risk to the city of Boston, 3,400 ha of wetlands were purchased in the Charles River Basin (U.S. Army corps of Engineers 1972), primarily because of their perceived value to society as purveyors of important services (Mitsch and Gosselink 2000).

All economic valuations of ecosystem services begin with the premise that an ecosystem in a specific state delivers – or is capable of sustaining – a given level of service. The task is then to estimate the marginal or total value of the service so provided. But the accuracy and/or precision (or both) of such an estimate depends not simply on the methods employed to estimate economic value, but on the accuracy of the initial estimate of the

level of service currently delivered or capable of being sustained. So the obvious question arises: to what extent can we estimate the level of a given service provided by a given ecosystem in a given state? Indeed, because economic valuations are supposed to inform ecosystem management, the question is not simply the level of service the system provides in its current state, but also the extent to which changes in state affect changes in service. In other words, the practical value of any economic valuation – irrespective of the method employed to obtain same – is linked directly to our ability to predict: (1) the current level of service provided by the ecosystem in question; and (2) how this level will change in response to changes in ecosystem state arising from different management regimes or decisions.

Here I address this question specifically in the context of a defined ecosystem type (wetlands) and a defined ecosystem service (flood control). My objective is to assess the current scientific evidence concerning the level of flood control service provided by wetlands. On the basis of a comprehensive review of the published scientific literature, I address two specific questions: (1) what is the level of the estimated flood control service delivered by wetlands; and (2) to what extent can we predict the estimated level of service from information about the state of the wetland ecosystem? The answer to the first question will I hope, provide useful information for ecological economists and could, in principle, allow them to bound estimates of economic value. The answer to the second question, on the other hand, will I hope provide both environmental scientists, managers and economists (among others) with valuable information on the uncertainty associated with any prediction about how the level of flood control service is expected to change under different wetland management regimes.

## **Materials and Methods**

### ***Flood control endpoints***

I consider a wetland to provide some level of flood control service if, in comparison to a “reference” situation (e.g. the absence of a wetland):

- i. Flooding is reduced,
- ii. Low flows are increased,
- iii. Water storage is increased,
- iv. Time to peak is increased, or
- v. Runoff is reduced

Associated with each of these criteria are a set of measurable attributes of the flood regime which I consider to be measurement endpoints or, more broadly, outcomes of interest (Table 2.1). These include: discharge, peak flow, low flow, mean annual flood, runoff, time to peak and storage (Table 2.1).

Wetlands are distinctly characterized ecosystem types for which the inundation of water becomes the dominant factor in determining the structure and composition of biotic communities in the wetland proper and adjacent non-wetland areas. For the purposes of this investigation, floodplain and semi-wetland areas which may only hold water seasonally or temporarily (not throughout the entire hydrological year) are also included. Non-natural wetlands like paddy fields were also included so long as impoundment or engineered flood control structures were not part of the system.

### ***Study design and effect size***

Studies on wetland flood control services span a wide range of approaches and methodologies (Table 2.2). Studies were classified based on several different attributes: (1) empirical versus modelling studies; and (2) study design, including Before/After (B/A), Control/Impact (CI) and Before/After-Control/Impact (BACI) designs. For B/A designs, one

or more hydrological endpoints were compared among multiple sampling units (e.g. wetlands) before and after an intervention (e.g. drainage). I compared average values of the endpoints before and after, with effect sizes given by the standardized mean difference of the endpoints before and after intervention (e.g. Lundin 1994- peak flow, before and after drainage).

For C/I designs, effect sizes were calculated based on the empirical relationship between the level of one or more measurement endpoints (Y) over a set of sampling units (e.g. sites) spanning a gradient of wetland presence (e.g. proportion of area as wetland, wetland number, etc.) (X). For example, Yang and colleague's simulated maximum and average flow (Y) and investigated the relationship between these parameters and the proportion of wetland that was restored in the watershed (X) (Yang et al. 2000). In C/I designs, the correlation coefficient between X and Y was used as the effect size.

Lastly, for BACI designs, one or more hydrological endpoints were compared among multiple sampling units (e.g. wetlands) before and after an intervention (e.g. beaver damming or drainage), with endpoint levels at impacted sampling units controlled to those at/in sampling unit(s) which were not impacted. For example, Nicholson et al. (1989) estimated a hydrological endpoint-(time to peak) in a peat bog before and after draining and compared to a control wetland which was not drained in Blacklaw Moss, Scotland. In such studies, effect sizes were calculated based on the size of the interaction – that is, the average difference between control (e.g. natural wetlands) and impact (e.g. wetland draining or dammed) sample sites in the difference between the level of flood control measurement endpoints before and after impact.

Certain (rare) study designs required a comparison between more than two groups. These studies usually took the form of control-impact (CI) designs along a spatial or geographical gradient of wetland presence (e.g. wetland area, coverage, number, etc.) representing in this case, multiple treatments. An example of such a study is in Starkweather Coulee subbasin, North Dakota where streamflow was simulated for various open wetlands (treatments) using 6 separate groups of increasing spillage thresholds (Vinning 1998). For study designs that were based on a comparison between multiple

treatments, eta-squared ( $\eta^2$ ) was used as the measure of effect size. This effect size measure is analogous to the coefficient of determination ( $r^2$ ) but used for data when analyzing more than two groups (ANOVA).

### ***Meta-Analysis***

Meta-analyses were performed as detailed by Borenstein et al. (2009) and Harrison (2011). In estimating effect sizes, I employed a random-effects model, as there is ample reason to expect that the true effect size will vary from study to study and that there is no true underlying effect size shared by all studies. Meta-regression was used as a meta-analytic tool to examine the impact of moderator variables on the dependent variable of effect size using regression based techniques. Meta-regression analyses and plots were created using the metafor package in R (Viechtbauer 2010).

Effect sizes were calculated using the standardized mean difference between groups, correlation coefficients or eta-squared ( $\eta^2$ ) (Table 2.2), as described above. All initial effect sizes were converted to correlation coefficients, thence to Fisher's z scale (an approximate variance-stabilizing transformation) as the principle effect size measure of interest (Borenstein et al. 2009). For presentation purposes, effect sizes have been reconverted to correlation coefficients.

### ***Meta-Regression***

I used mixed-effects meta-regression to model the effects of one or more potential predictors (moderators) (Table 2.3, for full candidate moderator description and associated metadata see Appendix B) on estimated effect sizes using the Empirical Bayes method to estimate heterogeneity (Morris 1983, Raudenbush and Bryk 1985). Candidate moderators included variables such as, for example, the study context (geographical location, duration and timing of the study, etc.), study design (e.g. Before/After versus Control/Impact), and the characteristics of the wetlands investigated (e.g. wetland type, wetland size, etc.). Fitted models were evaluated and assessed on the basis of Akaike Information Criterion (AIC),  $R^2$  analog, Deviance, Log-Likelihood, QE (residual heterogeneity) and QM (Test of moderators). Akaike's Information Criterion (AIC) scores, AIC differences and Akaike

weights were calculated to select the best model (Burnham & Anderson 2002). During model selection using an information-theoretic there was no overwhelming support for any one particular model, so model averaged estimates of candidate moderators were determined from multimodel inference (i.e. inferences based on the entire set of models)(Burnham & Anderson 2002).

On the basis of fitted meta-regression models, I estimated the predictive value of moderators, or sets thereof, with respect to observed effect sizes using individual studies as the sampling unit and analog  $R^2$  as a measure of predictive power. Heterogeneity was assessed using weighted sum of squares (Q); tau-squared ( $T^2$ ) (estimate of between studies variance); the proportion of observed variance that reflects real differences in effect size ( $I^2$ ); and ratio of total variability to sampling variability ( $H^2$ ).

To explore potential biases in the set of selected studies, I used funnel plots and fail-safe N.

### ***Multiple effect sizes per study***

Many studies generated multiple effect sizes, one for each of several different flood control endpoints. This introduces two potential problems: the (1) standard summary effect treats each effect size as an observation, thereby giving studies with multiple estimates more weight in the analysis than studies with only one estimate; and (2) the analysis ignores the possibility of within-study correlations among effect size estimates, potentially leading to an overestimated precision of the summary effect (Borenstein et al. 2009). To address this potential bias, I calculated the intra-class correlation (ICC) defined as

$$ICC = \frac{\sigma^2(b)}{\sigma^2(b) + \sigma^2(w)} [Eq. 1]$$

where  $\sigma^2(w)$  is the pooled variance in effect sizes within studies, and  $\sigma^2(b)$  is the between study variance.

I then calculated a 'synthetic effect size' which is a summary effect defined as the mean effect size in that study based for all estimated pollination indicators estimated as

well as a synthetic within-study variance based on the intraclass correlation using Eq. 5 of Borenstein et al. (2009, p. 228).

Using the Empirical Bayes method to estimate heterogeneity (Morris 1983, Raudenbush and Bryk 1985), once again meta-regression models were fitted to the data to examine the impact of candidate moderators on synthetic effect size.

### ***Study retrieval***

Literature searches were conducted in ISI Web of Science from October 2011 to April 2012. Search keywords included “flood control”, “flood prevention”, “flood attenuation”, “flood regulation”, “storm protection”, “flood mitigation”, “flood protection”, AND “wetland\*”. These search keywords were used in conjunction with the names of different wetland types (“bog”, “ephemeral”, “fen”, “flooded grassland\* and savanna\*”, “floodplain\*”, “peat\*”, “riparian”, “swamp” and “vernal”) (**A-Figure 2.1**). More studies were gathered by using Annex 1 of Bullock and Acreman (2003) (**B-Figure 2.1**), and using additional search terms “water storage capacity”, and “flow AND flood” (which were common to flood control studies found prior to this) and articles listed in the bibliographies of retrieved articles and appearing (on the basis of title and abstract) to be relevant to wetland flood control were reviewed (**C-Figure 2.1**).

### ***Inclusion criteria***

Selected studies: (1) report estimates of at least one measurement endpoint or indicator from the set shown in Table 2.1, and at least one wetland attribute from the set of candidate moderator attributes (Appendix B) on a set of sampling units (e.g. experimental replicates, sites, etc.); (ii) provide sufficient statistical information (mean, standard deviation or some estimate of precision, correlation, sum of squares, sample size for the various groups etc.) such that effect sizes could be estimated; (iii) must include a control treatment that allows one to infer the estimate of flood control service delivered under “treatments” such as, for example, wetland draining; and (iv) were published in a peer-reviewed scientific journal or in a government/institutional report that have been peer-

reviewed. Initial screening involved reading abstracts of all articles retrieved and eliminating those that, on the basis of information in the abstract, did not meet the four inclusion criteria (**233 studies, D-Figure 2.1**).

Sixty-seven studies of the 87 retrieved candidate studies were excluded from quantitative analysis because:

- (i) No online or print versions were available (this was the case for many USGS sources), only an abstract was available. They may, however, still have provided useable statements about the impacts of wetlands on flood control services(**23 studies, E-Figure 2.1**);
- (ii) inadequate study design or insufficient statistical data to estimate effect sizes (**39 studies, F-Figure 2.1**);

Of these studies excluded from the quantitative (weighted) meta-analysis, 5 were included in a separate unweighted meta-analysis and a further 62 studies were included in a separate qualitative analysis.

### ***Unweighted meta-analysis***

Five retrieved articles provided quantitative estimates of the difference between control and experimental groups, but did not report associated measures of precision (e.g. standard errors, confidence intervals) or sample sizes. These studies were included in an unweighted meta-analysis, with unweighted effect sizes calculated using Haxton and Findlay (2008, eq. 1 - a variation on Osenberg et al. (1997), eq. 4) and a summary effect was calculated using Haxton and Findlay (2008, eq. 2).

### ***Qualitative analysis test***

For some studies, insufficient information was provided that would permit estimates of effect size. For these studies, I employed a variant of the more usual vote-counting (Harrison 2011) method. Instead of classifying studies on the basis of significant or non-

significant type I error rates, I used the author's own statements about the significance of their results. An author statement which, in my view, would be interpreted as providing evidence that pollinator populations positively contributed to agricultural productivity, was given a positive score (+1). By contrast, an author statement which, in my view, would be interpreted as providing evidence that pollinator populations did not contribute to agricultural productivity, was given a negative (-1) score. I then used a sign test to test the null hypothesis of an equal distribution of negative and positive scores (Borenstein et al. 2009). Studies were assigned a value of +1 only if it was clearly stated that a positive effect was detected. If the effect was negligible or non-existent by the author's own account, it was given a -1 score. Only one score was assigned per study. Studies that had multiple outcome statements in conflicting directions were not included in the qualitative analysis.

## Results

In total, 40 effect sizes were calculated from 20 studies.

Weighted meta-analysis yielded a small positive overall mean effect size of  $0.35 \pm 0.12$  (1 SE),  $k = 40$ ,  $p = 0.0046$  (95% CI = [0.11, 0.59] (Figure 2.2), corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.33 (95% CI, [0.03, 0.58]). All five measures of heterogeneity indicated substantial variation in effect size (Table 2.4).

### *Mixed effects models*

Including all effect sizes ( $k=40$ ), five predictors (Table 2.5) showed informative bivariate associations with study effect size: wetland type (Floodplain vs. surface water depression/slope vs. ground water depression/slope etc.) (Figure 2.3), study control (parameters fixed or not) (Figure 2.4), study type (empirical, modelled or modelled from empirical data) (Figure 2.4), publication year and wetland order (floodplain vs. headwater wetland). For complete model results see Appendix C.

On the basis of the original examination of the bivariate effects of individual candidate moderators, I defined a set of 16 candidate models involving linear combinations of the moderators shown in Table 2.5, constrained by the requirement that, for any model, the number of estimated parameters must be fewer than 5, including the intercept. This condition was imposed to ensure that the ratio of sample size to the number of predictors was around 10, sufficient – at least in principle – to ensure reasonable model stability and/or sufficient precision of estimated coefficients (Vittinghoff et al. 2005, p. 149). Of these 16, thirteen had  $\Delta AICs < 7$  (Table 2.6), with the best model including wetland type and publication year (Table 2.6). As there was no overwhelming support for any one model (Table 2.6) estimated coefficients were based on model averaging (Figure 2.5).

A second sub sample of effect sizes ( $k=25$ ) was defined to include reported estimates of three additional moderators: basis of inference, wetland study and wetland area, for the original sample of 40, had too many missing values. For this sub-sample, five moderators (Table 2.7), including the basis of inference (whether inference was drawn from

a system with a wetland and one without, drainage, paired or multiple wetlands or the presence of a beaver dam)(Figure 2.6), showed informative bivariate associations. While wetland area had no sole influence on effect size it did have an interaction with study type (reducing AIC from 76.84 to 72.24, Analog  $R^2$  0.27) and study control (reducing AIC from 76.84 to 73.34, Analog  $R^2$  0.2). For full model results see Appendix D.

Due to the constraint mentioned above (Vittinghoff et al. 2005, p. 149), regarding the number of estimated parameters to ensure reasonable model stability and/or sufficient precision of estimated coefficients, in this reduced sample the number of estimated parameters must be fewer than 3 and the only model that meets this requirement is the one including publication year (1 parameter plus intercept).

### ***Unweighted meta-analysis***

The estimated unweighted effect size (N = 5 studies) was 1.97, which, if I treat this as analogous to Cohen's d, yields an estimated correlation of 0.7.

### ***Qualitative analysis test***

Of the 62 studies not included in the quantitative meta-analysis, 15 indicated that wetlands had a negative or negligible effect on flood control capacity, while 47 indicated a positive effect (two-tailed sign test,  $p < 0.0001$  – see Borenstein et al. (2009)).

### ***Publication Bias***

Visual inspection of the funnel plot (Figure 2.7) of the standard error of the estimate versus z-transformed effect size suggest little bias of the type such plots are supposed to uncover (see Borenstein et al. 2009) but substantial heterogeneity in effect size. A formal test for funnel plot asymmetry based on the random-effect regression test also suggested little asymmetry ( $z=1.63$ ,  $p=0.1$  and, one presumes, little publication bias). However, one should interpret these results cautiously; regression tests for asymmetry have comparatively low power (Borenstein et al. 2009).

Using Duval and Tweedie's Trim and Fill approach (2000a, 2000b) the estimated number of missing studies on the left size of the funnel plot is zero. Hence, my estimate of the effect size and the estimate of an unbiased effect size as calculated by Duval and Tweedie's Trim and Fill approach are very similar, such that no further augmentation was required to render the funnel plot more symmetric.

### ***Fail-Safe N***

Rosenberg's (2005) Fail-Safe N (3186; observed significance level < 0.0001, target significance level = 0.05), as well as Rosenthal's (1979) Fail-safe N (1869 -Observed Significance Level: <0.0001, Target Significance Level: 0.05) both suggest that the impact of bias is small.

### ***Multiple effect sizes per study***

Based on a synthetic effect size using the correlation among outcomes within studies (Table 2.8, ICC = 0.97, Figure 2.8), the weighted meta-analysis increased to  $0.44 \pm 0.19$  (1 SE),  $N = 20$ ,  $p = 0.02$  (95% CI = [0.07, 0.82] (Figure 2.9), corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.42 (95% CI, [-0.03, 0.73]).

Treating synthetic effect sizes as the dependent variable, I investigated the association with several candidate moderators at the study level ( $k=20$ ). Only study control (parameters fixed or not) showed a bivariate association with effect size (Table 2.9). For full model results see Appendix E. In this analysis, statistical power is dramatically reduced as a result of the reduced sample size. Consequently, only comparatively strong associations will be detected.

## Discussion

My meta-analysis of the published literature provides compelling evidence that, overall, consistent with conventional wisdom, on average wetlands do indeed have a positive effect on flood control by reducing the frequency and magnitude of floods, reducing runoff, increasing low flows, and increasing water storage. However, there was substantial heterogeneity in estimated effect sizes among studies, with some studies indicating negligible or even negative effects (e.g. increasing dambo area increased mean annual flood and decreased low flow (Drayton 1980), peak flows were higher before draining (Lundin 1994) and peak flow increased with wetland area (Frazier and Page 2009)). My analysis indicates that, overall, a greater level of flood control services was provided in groundwater depressions or slopes versus surface water depressions or slopes or floodplain wetlands and based on my sample, in general, with headwater wetlands versus floodplain wetlands. Greater provisioning was also associated with modelling studies versus empirical; empirical studies that experimentally fixed certain parameters (e.g. the rate of discharge into a wetland) versus those that don't; and studies which inferred flood control from a control situation where a wetland was present to a situation where no wetland was present, rather than compare paired/multiple wetlands, wetlands with a beaver dam or without, or wetland drainage. Lastly, the size of reported effects increased slightly through time. However, despite informative associations with a number of moderators, overall predictive power of even the best model was comparatively modest, with most (about 72%) of the variation in estimated effect sizes remaining unexplained.

Estimated effect sizes were larger for headwater wetlands than floodplain wetlands. By contrast, Bullock and Acreman (2003), on the basis of their systematic review of the literature concluded:

“Most, but not all studies (23 of 28) show that floodplain wetlands reduce or delay floods, with examples from all regions of the world. This same influence on floods is also seen, but less conclusively (30 of 66) for wetlands in the headwaters of river systems (e.g. bogs and

river margins). A substantial number (27 of 66) of headwater wetlands increased flood peaks”.

Indeed, their study noted cases where wetlands actually increase floods, act as a barrier to recharge, or reduce low flows (Bullock and Acreman 2003). Only 4 studies in my analysis concerned floodplain wetlands, and, given the large heterogeneity in effect sizes, it is entirely possible that this effect is not robust, and may well reflect the specific features of this small sample of floodplain wetland studies. Certainly the potential exists that certain floodplains (as well as headwater wetlands) may provide extensive flood control services due to their size or location within a watershed (Bengston and Padmanabhan 1999). Groundwater depressions or slopes likely had a larger bivariate influence on effect size than surface water depressions or slopes because of the ability to infiltrate excess water into the ground instead of releasing stored waters as surface runoff.

Modelling studies had, on average, larger estimated effect sizes than empirical studies. Uncertainty in modelling reflects not only uncertainty in parameter estimates, but also more fundamental uncertainty associated with the degree to which any model fully captures underlying processes. Choosing any model introduces epistemic uncertainty associated with model structure and the model structure’s ability to capture parameter estimates. Certainly the focus in modelling will be on processes which are considered to be better understood; if other largely processes are at work, they can only be accommodated in the model through noise. The result may well be that the effects of known processes are exaggerated. Certainly those involved in modelling wetland function admit the problem: Yang et al. (2010), for example, note that “It has been a challenge to characterize wetland functions using a watershed hydrological model”. Whatever the reason for the apparent bias, my results suggest that modelling studies may well overestimate the flood control services delivered by wetlands.

Studies which modelled different simulations with the presence of a wetland or a case within the same basin without the wetland(s) had, on average, larger estimated effect sizes than those studies which based inference on paired/multiple wetlands, damming or drainage. The inference situation where a comparison of the same basin, with or without a

wetland showing the highest effect is logical considering that this inference removes any noise caused by other non-wetland specific elements (e.g. surrounding vegetation, soil saturation, and geospatial location). By definition this basis of inference has stability of model parameters (Bullock and Acreman 2003) and the response between outputs can be attributed wholly to the presence of the wetland.

The impact of draining wetlands on flood control service delivery is one of controversy in the hydrological literature (Robinson 1990a). Existing data indicates no clear generalized model of how drainage affects the flood control services delivered by wetlands. Certain studies have concluded draining wetlands contributes more to streamflow than undrained wetlands (Malcolm 1979, Jackson 1987) while other studies have demonstrated draining to lead to reduced discharges (Lundin 1994). One possible explanation for these heterogeneous results is that upstream wetlands are more suited to serve and store floodwaters (temporarily releasing them slowly downstream). In this circumstance, drained upstream or head water wetlands will be more likely to have a negative effect by increasing flow rates. On the other hand, downstream wetlands which may already be saturated with water from upstream sources, such that draining may provide short term flood water storage capacity. Thus, drainage may increase or decrease peak flow relative to undrained land, depending on site characteristics like soil properties and the soil water regime prior to drainage (Robinson 1990b).

There were three moderators that were expected to show an association with estimated effect sizes, but did not:

*Wetland number and size.* Wetland size is often cited as an important determinant of the level of flood control services delivered by wetlands (Ogawa 1986, Demissie and Khan 1993, Bengston and Padmanabhan 1999, EPA 2006). Yet, my results found no sole interaction with wetland number and size on the level of flood control service (effect size). An empirical study in the Red River Valley of Manitoba investigated the role of wetlands in regards to flood impacts and the number and size of wetlands also provided no clear indication of wetland role in alleviating floods (Juliano 1999) also (potentially) indicating the size and number of wetlands had no influence on the level of flood control service.

However I did find an interaction between wetland size and other predictors, notably study type and study control. It is possible given this result, that wetland number or size may only be a determinant of flood control services given certain situations like: the type of local weather witnessed, location (relative to other wetlands and water tributaries), and how one conducts their study (empirical or modelled, fixing parameters and study inputs etc.)

*Wetland Study.* Wetland studies were classified according to the Bullock and Acreman (2003) classification scheme. While there was no *a priori* evidence to suggest that category of wetland study would have an influence, nonetheless one might expect that effects sizes might be greater for conceptual catchment models than a long-term hydrograph which is less likely to capture short term responses to floods. Conversely, those studies which focused on individual water balance component or hydrological processes (component processes) might be expected to show a larger effect size owing to the fact these sorts of studies isolate a certain component of the system which should, in theory, reduce noise. It may be likely that even employing a wetland study on an isolated component of a system may still be too complex to hope to get an accurate signal of the represented data.

*Hydrological Endpoints.* According to Bullock and Acreman (2003) “Published studies in wetland hydrology are not consistent in their attention to different measures; it is possible to find one study analysing the return period of flood peaks extracted from a 20 or 30 year flow records, and another analysing the flood volume of a single event, with both drawing conclusions on wetland influences on floods”. Irrespective of the endpoint or the timing of measurement, it appears that this categorization does not have a large influence on the obtained hydrological conclusion. This analysis then suggests that flood control services do not significantly alter or depend on the type of hydrological endpoint that is measured.

### ***Sources of uncertainty***

*Study retrieval.* The sample of assessed studies was constrained in several important respects. In particular, Bullock and Acreman (2003), the largest source of information for

historical studies, included many sources from books and US Geological Service reports for which tracking down the original report proved very difficult given existing time and resource constraints. Such studies were, on average, older than studies included in the current analysis. Based on my finding of the association of estimated effect sizes with publication year, this under-representation of earlier studies may have led to an overestimate of overall effect sizes (in my case, likely associated with a shift from empirical studies to modelled studies through time), as has been reported in other research areas (e.g. in mental health (Fusar-Poli et al. 2012) or cancer clinical trials (Engelbrecht 2002) research), as well as (potentially) biased estimates of the effects of candidate moderators. On the other hand, estimates of fail-safe N are large (e.g. 1869-3186) suggesting (to the extent that one can rely on such estimates – see, for example, Scargle 2000) that non-inclusion of such studies is not expected to have a substantial impact on my results.

*Characterization of moderator variables.* Nominal/ordinal level variables, and the corresponding coding of specific studies, has a certain element of uncertainty relating to differences among studies in the extent to which the information required to categorize studies is reported. For example, although the three different levels of wetland study (Conceptual catchment model, Long-term hydrograph and Component process) should be readily distinguishable in practice, in principle ambiguity exists because, for example, wetland studies may not make it clear whether only a single water balance component or hydrological processes was estimated, or whether the reported results are integrated over several balance components or processes. By definition a component process wetland study is the investigation of an individual water balance component or hydrological process (Bullock and Acreman 2002) and therefore it is at the discretion of the researcher to determine if a given wetland study is investigating a single water component or whether the study incorporates more components in the form of a conceptual catchment model or long-term hydrograph. This decision will ultimately lead to some uncertainty and bias associated with the resulting classification. If there is uncertainty as to which class of a nominal (or ordinal) level variable a particular study falls within, the result will be a blurring of levels, and a reduction in the associated estimated effect size, if indeed there is a true

relationship. Under this type of uncertainty then, the strength of associations with specific nominal moderators will be underestimated, as will the estimated predictive power of the associated model.

Moreover, all nominal/ordinal variables – and their associated levels - are arbitrary to some degree, and there is no guarantee that the adopted system systematically captures the existing range of variation in a highly repeatable fashion. In this study, I adopted the classification system developed Bullock and Acreman (2003) for wetland type, wetland study and basis of inference. As such, any errors, uncertainties or infelicities associated with this classification system will be propagated here.

It is also evident that estimated effect sizes depend on context. For example, for most studies that investigated the flood control function of wetlands during extreme weather events (for example see Jung et al. 2011), the size or attributes of the wetland has little or no predictive value with respect to estimated effect size.

Also, prediction within a study requires that appropriate predictors (moderators) be identified. Prediction across studies might mean that the factors that are responsible for differences among wetlands, have not been identified or that I have treated them naively.

### ***Implications***

My results have several implications. First, I have shown a consistent positive effect of wetlands to deliver flood control services. I have also shown that, on average, greater levels are associated with headwater wetlands rather than floodplains. There is, therefore, reasonably strong evidence that degradation of wetlands (due to drainage, cultivation etc.) is very likely to have a negative effect on the natural flood control protection that humans currently benefit from. Maintaining natural flood control services will then depend on either reversing the wetland degradation, or adopting appropriate – but almost certainly more costly - compensation strategies (Juliano 1999) for which, in low-income areas the technology for these strategies are not as readily available (Millennium Ecosystem Assessment 2005b).

*Second*, my results indicate that detected associations with several moderators notwithstanding, the predictive power of even the best models is modest at best. This,

combined with the observed heterogeneity of effect sizes, means that, in the absence of considerably more detailed *in situ* information about the specific wetland(s) of interest, any estimate of the current level of flood control service delivered by a wetland; or the expected change in service provisioning under alternative management actions, will have a large associated uncertainty.

This finding has several implications for economists, environmental scientists and resource managers. For ecological economists, there is already a vigorous debate about appropriate methodologies for estimating the economic value of ecosystem services, especially those for which, at present, no market exists (see e.g. Wilson and Carpenter 1999, Bockstael et al. 2000, Howarth and Farber 2002). Moreover, estimations of the economic value of flood control services and wetlands is highly variable or uncertain (Gren et al. 1995, Woodward and Wui 2001) depending on a number of factors like the productivity of a unit area of wetlands based on the remaining wetlands (Costanza et al. 1989), valuation method (Lambert 2003), and where the wetland is found in the landscape (Mitsch and Gosselink 2000). To this methodological conundrum must now be added the arguably even more fundamental constraint that our ability to predict the level of flood control service currently provided by a particular wetland or wetland complex is low. Even more problematic are predictions about how the level of services delivered is likely to change under different management scenarios. The consequence is that any estimation of the economic value of the level of flood control services delivered by a wetland will have large, even very large, uncertainty. To the extent that economic valuation is employed as a criterion for decision-making about wetland management, then, such decisions must take explicit account of the high degree of uncertainty. Moreover, substantially reducing such uncertainty will require considerably more detailed scientific knowledge about the specific system under consideration.

The findings have several different implications for the development and implementation of market-based instruments (MBIs) for conserving wetlands or, more generally, for the payment for flood control (or any other) services. First, the development of MBIs for a particular ecosystem and service (or, possibly, set of services) requires, first

and foremost, that the level of the service(s) currently provided be estimated. Anderson et al. (2010) note that "...It is frequently not enough to know that ecosystems are valuable; it is often necessary to know how valuable they are relative to other outcomes, and how that value may be affected by alternative management actions and to inform trade-off decisions". Knowing how valuable an ecosystem is in a given state (or under a given management action) necessarily implies knowledge of how much of a particular service it will deliver. For example, the Conservation Effects Assessment Project—Wetlands National Component (CEAP–Wetlands) was developed by the U.S. Department of Agriculture (USDA) to evaluate effects of conservation practices on ecosystem services including carbon sequestration for climate stability, groundwater recharge, runoff and flood attenuation, water storage, nutrient and contaminant retention, and wildlife habitat (Euliss, Jr 2011). It requires that the level of these services be estimable using information on the biophysical attributes of wetland and associated hydrological networks, especially that which can be remote-sensed (Feng et al. 2009).

MBIs are concerned largely with protecting quantitative estimates of the value of ecosystem services per unit service provided (or some proxy thereof, for example, the annual per hectare value of wetlands (e.g. Olewiler 2004, Molnar et al. 2012). Another example, Troy and Wilson (2006) developed a value transfer model for three different spatial scales and locations in the U.S. In each case, value estimates (annual value per unit area for a given service) are derived directly from estimates of the level of a particular service delivered by a particular land-use class and set of aquatic resources. A quantitative estimate of total value is then obtained by multiplying the unit economic value by the estimated amount of service provided by the system in its current states and, ideally, under alternate states. Yet my results suggest that, in the absence of highly detailed, ecosystem- and service-specific biophysical information, any quantitative estimate of the level of service provided – especially under alternate states/management regimes -may be so imprecise that the estimate itself is of comparatively little quantitative value.

To what extent can environmental science deliver on this requirement to estimate a level of service (or sets thereof) and how a management action might affect this level? My

results suggest that, in general, poorly. While it seems clear that, on average, there are some flood control services delivered by wetlands, the observed large heterogeneity in effect sizes strongly suggests a strong context-dependence. Moreover, as I have shown, those variables that apparently have some predictive value do not simply relate to the biophysical attributes of the ecosystem under investigation, but the endpoints (and associated ecological functions) chosen to characterize the service in the first place, as well as the type of experimental design adopted. Moreover, although there are variables with some comparatively small predictive value, even when combined, overall predictive value is low. This conclusion holds for what would appear to be one of the most intensively studied combinations of ecosystem and service; it does not, therefore, foretell well for the many more ecosystems and services that are much more poorly studied.

The consequences of the above are, that at present – and probably for the foreseeable future – are:

- (1) Given a particular ecosystem (or set thereof) and service (or set thereof), environmental science may be able to provide some rough estimate of the level of service currently provided if the associated ecological function(s) are few and well characterized, and we can agree on what endpoints ought properly be used to characterize these functions.
- (2) Given a set of possible management actions, environmental science may be able to provide semi-quantitative ranking of the effect on those ecological services satisfying the criteria in (1) above, if the relationship between management action and the levels of associated functions is well characterized. If these conditions are not satisfied, then an ordinal ranking is likely the best one can do with any degree of confidence.
- (3) If more refined (that is, higher resolution and precision) estimates of the level of service are required, it is very likely that marked enthusiasm (and resources) for more detailed scientific research are required. In this case, in order to improve the prediction of wetland services, there needs to be more study of (context-

specific) wetlands. If this condition is not met, alternate strategies – perhaps of the command and control variety – may be the more realistic alternative.

My hope is that this project is a benchmark study representing a synthesis of quantitative data from the environmental science literature regarding a particular service (flood control function) of a particular ecosystem type (wetland). In principle, this general, but context-dependent approach can be applied to any ecological function and ecosystem to begin to assemble a library of current syntheses on what is, and isn't, known about ecosystem services. At the same time, one could imagine the building of a library of syntheses of the economic valuation of particular services in particular ecosystems. Cross-referencing these libraries (on the basis of ecosystem service and ecosystem type) would then provide decision-makers with a large part of the evidence required to make informed evidence-based decisions on wetland conservation and management.

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## Tables

Table 2.4. Flood control criteria and associated measurement endpoints and indicators.

| Flood control criteria              | Measurement endpoint                                     | Indicator                              | Units  | Example Reference         |
|-------------------------------------|--|--|--|---------------------------|
| <b>Reduction in Flooding</b>        | Flow/Discharge   | Average, Daily, Instantaneous, Maximum | $l/s, ft^3/s, km^3, m^3/s, m^3 s^{-1} \dots$                         | Wu and Johnston (2008)    |
|                                     | Peak Flow  | Average, Maximum, Minimum              | $m^3 s^{-1}, 1 s^{-1} km^{-1}, m^3/s, 1 s^{-1} ha^{-1}, \%dQp \dots$ | Jackson (1987)            |
|                                     | Mean Annual Flood  | Instantaneous, Maximum                 | Cumecs, $Q_{bar}/Area$   | Drayton et al. (1980)     |
|                                     | Peak Flow to Precipitation Ratio                         | Average, Peak, Total                   | $Q_p/P_a, Q_p/P_{pr}, Q_p/P_t$                                       | Demissie and Khan (1993)  |
|                                     | Flood flow volume to total precipitation ratio           |  | $V/p_t$  | Demissie and Khan (1993)  |
| <b>Increase in Low Flow</b>         | Low Flow   |  | $Q_{75}, Q_{95}, Q_{99}, Q_{355} \dots$                              | Drayton et al. (1980)     |
| <b>Reduction in Runoff</b>          | Runoff   | Peak, Surface, Total                   | $mm, s^{-1} km^2, m^3/s \dots$                                       | Jung et al. (2011)        |
| <b>Increase in Time to Peak</b>     | Time to Peak   | Flow, Runoff                           | Days, Hours ...  | Nicholson et al. (1989)   |
|                                     | Peak Hourly Flow as a Proportion of the Total Storm Flow |  | $Q_p$  | Nicholson et al. (1989)   |
| <b>Increase in Storage Capacity</b> | Storage  |  | $mm, mm^3 \dots$   | Woo and Waddington (1990) |

Table 2.5. The effect size measure employed for different flood control service study designs and methods of calculating pollination effect size for different statistical estimates and study designs.

| Basis of Inference                       | Study Design  | Study Type             | Effect Size measure          | Reference Examples   |
|--|---|------------------------|------------------------------|--|
| Effect size based on correlation         | Control-Impact  | Empirical and Modelled | Correlation coefficient (r)  | Ogawa and Male (1986), Bullock (1992)                                |
| Effect size based on two means           | Before-After; Control-Impact; Before-After/Control-Impact | Empirical and Modelled | Standardized mean difference | Lundin (1994), Smakhtin and Batchelor (2005), Balek and Perry (1973) |
| Effect size based on more than two means | Control-Impact  | Modelled               | Eta-squared ( $\eta^2$ )     | Jung et al. (2011)   |

Table 2.3. Candidate flood control service moderators, and associated levels (for categorical moderators).

| <b>Predictor Variables</b>   | Variable type   | Levels   |
|------------------------------|-----------------|--|
| <b>Study type</b>            | Ordinal         | <i>Empirical, Modelled, Modelled from Empirical Data</i>   |
| <b>Wetland type</b>          | Nominal         | <i>Surface Water Depression/Slope And Groundwater Depression/Slope, Surface Water Depression/Slope, Groundwater Depression/Groundwater Slope, Floodplain</i> |
| <b>Study design</b>          | Nominal         | <i>Before-After, Control-Impact, Before-After/Control-Impact</i>   |
| <b>Wetland study</b>         | Nominal         | <i>Conceptual catchment model, Water balance, Long-term hydrograph, Single event hydrograph, Trend analysis in time series, Component process</i>            |
| <b>Local term</b>            | Nominal         | <i>Paddy Field, Dambo, Marsh, Pakihi, Bog, Peat, Fen, Wadi, Wetland</i>  |
| <b>Flood event</b>           | Ordinal         | <i>Natural, Extreme</i>  |
| <b>Study control</b>         | Ordinal         | <i>Parameters not fixed, Parameters fixed</i>  |
| <b>Basis of inference</b>    | Nominal         | <i>With/out, Drained, Pair, Multiple, In-out, Same, Dam-No Dam, Comp<sup>a</sup></i>   |
| <b>Hydrological endpoint</b> | Nominal         | <i>Discharge, Peak Flow, Low Flow, Runoff, Time to Peak</i>  |
| <b>PSHB threshold</b>        | Ordinal         | <i>No threshold effect, Threshold effect</i>   |
| <b>Wetland order</b>         | Ordinal         | <i>Headwater Wetland, Floodplain</i>   |
| <b>Country</b>               | Nominal         |  |
| <b>Sample size</b>           | Interval        | <i>Continuous...</i>   |
| <b>Wetland area</b>          | Interval (ha)   | ...  |
| <b>Study size</b>            | Interval (ha)   | ...  |
| <b>Year of study</b>         | Interval (Year) | ...  |

Table 2.6. Heterogeneity of Effect Size (Q Test for Heterogeneity,  $T^2$  is the variance of the true effect sizes,  $T$  is the standard deviation of the true effects,  $I^2$  is the proportion of observed variance that reflects real differences in effect size and  $H^2$  is the ratio of total variability present to sampling variability).

| Heterogeneity measure   | Outcome Statistic |
|---|-------------------|
| Test for Heterogeneity (Q, df=39):                                  | 336.8(p<.0001)    |
| Tau-squared estimate of the total amount of heterogeneity ( $T^2$ ) | 0.51              |
| Tau standard deviation estimate of total heterogeneity (T)          | 0.71              |
| % of total variability due to heterogeneity ( $I^2$ )               | 99.1%             |
| Total variability/sampling variability ( $H^2$ )                    | 110.4             |

Table 2.5. Bivariate associations between estimated effect size (ES) and candidate moderators based on a sample of 40 effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE) and test of moderators (QM), and associated type I error rates ( $p$ ).

| Model               | Log-Likelihood | AIC   | $R^2$ analog | QE     | $p$    | QM   | $p$  |
|---------------------|----------------|-------|--------------|--------|--------|------|------|
| ES~Null             | -46.73         | 97.45 |              |        |        |      |      |
| ES~Wetland type     | -43.01         | 96.01 | 0.12         | 187.72 | <.0001 | 6.89 | 0.08 |
| ES~Study control    | -45.12         | 96.25 | 0.06         | 251.34 | <.0001 | 2.89 | 0.09 |
| ES~Study type       | -44.69         | 97.38 | 0.06         | 334.50 | <.0001 | 1.98 | 0.16 |
| ES~Publication year | -45.69         | 97.38 | 0.03         | 252.64 | <.0001 | 1.91 | 0.17 |
| ES~Wetland order    | -45.70         | 97.40 | 0.03         | 307.51 | <.0001 | 1.9  | 0.17 |

Table 2.6. Bivariate associations between estimated effect size (ES) and multiple candidate models involving linear combinations of the top five moderators. Shown are model log likelihood, Second order Akaike Information Criterion (AICc),  $R^2$  analog, Delta AIC, Akaike weights and evidence ratios.

| Model Rank | Model  | Log-Likelihood | AIC   | AIC <sub>c</sub> | $R^2$ analog | $\Delta$ AIC | Weight ( $w_i$ ) | Evidence Ratio |
|------------|--|----------------|-------|------------------|--------------|--------------|------------------|----------------|
| 1          | ES~Wetland type+Publication year             | -39.34         | 90.69 | 92.45            | 0.28         | 0.00         | 0.47             |                |
| 2          | ES~Study type+Wetland order                  | -42.06         | 94.11 | 95.25            | 0.17         | 2.80         | 0.12             | 4.05           |
| 3          | ES~Study control                             | -45.12         | 96.25 | 96.57            | 0.06         | 4.12         | 0.06             | 7.84           |
| 4          | ES~Wetland type+Study control                | -41.61         | 95.23 | 96.99            | 0.17         | 4.54         | 0.05             | 9.67           |
| 5          | ES~Wetland type                              | -43.01         | 96.01 | 97.15            | 0.12         | 4.70         | 0.04             | 10.48          |
| 6          | ES~Publication year                          | -45.69         | 97.38 | 97.70            | 0.03         | 5.25         | 0.03             | 13.80          |
| 7          | ES~Wetland order                             | -45.70         | 97.40 | 97.72            | 0.03         | 5.27         | 0.03             | 13.92          |
| 8          | ES~Study control+Publication year            | -44.69         | 97.38 | 98.05            | 0.06         | 5.59         | 0.03             | 16.38          |
| 9          | ES~Study type                                | -44.69         | 97.38 | 98.05            | 0.06         | 5.59         | 0.03             | 16.39          |
| 10         | ES~Study type+Publication year+Wetland order | -42.15         | 96.29 | 98.05            | 0.14         | 5.60         | 0.03             | 16.44          |
| 11         | ES~Study control+Wetland order               | -44.70         | 97.40 | 98.07            | 0.06         | 5.61         | 0.03             | 16.54          |
| 12         | ES~Study control+Study type+Wetland order    | -42.17         | 96.34 | 98.10            | 0.14         | 5.65         | 0.03             | 16.86          |
| 13         | ES~Publication year+Wetland order            | -44.78         | 97.56 | 98.23            | 0.06         | 5.77         | 0.03             | 17.92          |

Table 2.7. Bivariate associations between estimated effect size (ES) and candidate moderators based on the sub-sample of 25 effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE) and test of moderators (QM), and associated type I error rates ( $p$ ).

| Model                 | Log-Likelihood | AIC   | $R^2$ analog | QE     | $p$    | QM    | $p$    |
|-----------------------|----------------|-------|--------------|--------|--------|-------|--------|
| ES~Null               | -33.13         | 70.26 |              |        |        |       |        |
| ES~Study type         | -24.41         | 56.81 | 0.52         | 210.58 | <.0001 | 18.50 | <.0001 |
| ES~Study control      | -28.10         | 62.19 | 0.35         | 143.11 | <.0001 | 9.87  | 0.002  |
| ES~Basis of inference | -28.61         | 67.21 | 0.25         | 191.67 | <.0001 | 8.66  | 0.03   |
| ES~Wetland type       | -29.42         | 68.84 | 0.19         | 133.58 | <.0001 | 7.03  | 0.07   |
| ES~Publication year   | -31.44         | 68.88 | 0.10         | 142.69 | <.0001 | 3.11  | 0.08   |

Table 2.8. Effect size and the associated within-study intraclass correlation (ICC) used to estimate within-study variance. Blank fields indicate studies for which only one effect size was calculated.

| Study | Study Name       | Effect Size | Correlation | Variance |
|-------|------------------|-------------|-------------|----------|
|       |                  | $z$         | ICC         | $V_z$    |
| 1     | Wang             | 0.02        |             | 0.03     |
| 2     | Nyssen           | 0.29        | 0.20        | 0.04     |
| 3     | Drayton          | -0.50       | 0.37        | 0.02     |
| 4     | Demissie         | 0.31        | 0.14        | 0.01     |
| 5     | Jackson          | 1.00        |             | 0.03     |
| 6     | Balek            | 0.07        | 0.27        | 0.03     |
| 7     | Smakhtin         | 0.07        | 0.32        | 0.02     |
| 8     | Ogawa            | 1.45        |             | 1.00     |
| 9     | Yang             | 3.60        | 0.07        | 0.13     |
| 10    | Bullock          | 0.14        |             | 0.01     |
| 11    | Yu               | 1.39        |             | 0.06     |
| 12    | Nicholson        | 0.68        | 0.35        | 0.02     |
| 13    | Frazier          | 0.05        | 0.03        | 0.11     |
| 14    | Lundin/Bergquist | 0.24        |             | 1.00     |
| 15    | Lundin           | 0.003       | 0.59        | 0.002    |
| 16    | Iritz            | 0.63        |             | 1.00     |
| 17    | Wu               | 0.18        | 0.93        | 0.0009   |
| 18    | Vinning          | 0.16        |             | 0.01     |
| 19    | Jung             | 0.01        | 0.13        | 0.03     |
| 20    | Acreman          | 0.13        | 0.08        | 0.11     |

Table 2.9. Bivariate associations between estimated effect size (ES) and candidate moderators based on the sample of 20 synthetic effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE) and test of moderators (QM), and associated type I error rates ( $p$ ).

| <b>Model</b>     | Log-Likelihood | AIC   | $R^2$ analog | QE     | $p$    | QM   | $p$  |
|------------------|----------------|-------|--------------|--------|--------|------|------|
| ES~Null          | -25.19         | 54.38 |              |        |        |      |      |
| ES~Study control | -24.57         | 55.15 | 0.01         | 193.01 | <.0001 | 1.22 | 0.27 |
| ES~Wetland order | -24.81         | 55.62 | 0            | 183.58 | <.0001 | 0.77 | 0.38 |
| ES~Study design  | -25.23         | 56.47 | 0            | 194.99 | <.0001 | 0.01 | 0.92 |
| ES~Flood event   | -25.24         | 56.48 | 0            | 198.67 | <.0001 | 0.00 | 0.99 |
| ES~Study type    | -24.24         | 56.49 | 0            | 180.47 | <.0001 | 1.90 | 0.37 |
| ES~Wetland type  | -24.24         | 56.49 | 0            | 180.47 | <.0001 | 1.90 | 0.37 |

## Figures

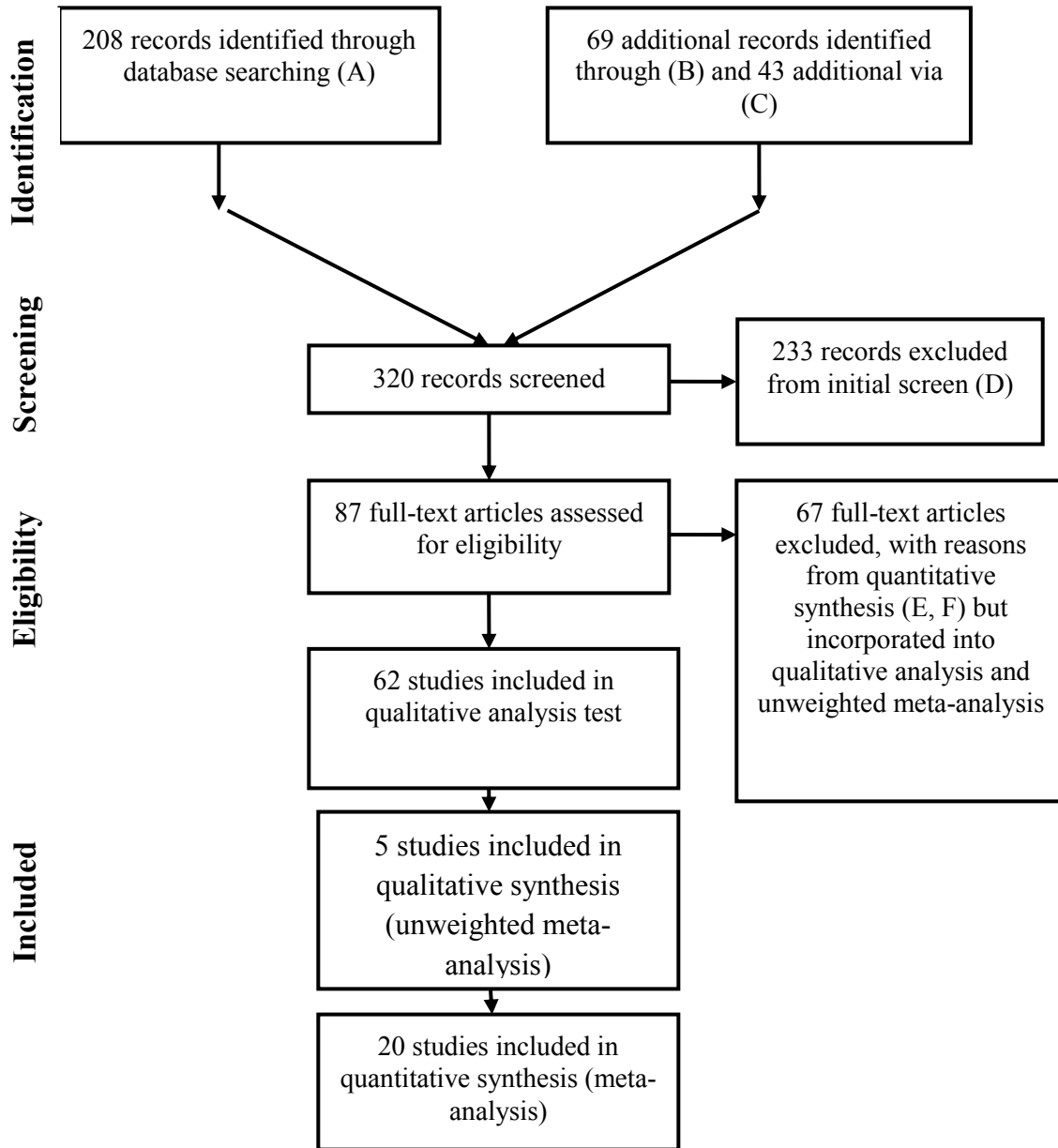


Figure 2.1 .Flow chart indicating study identification based on study retrieval and screening and eligibility according to stated inclusion criteria and those studies included in a quantitative (weighted) meta-analysis and qualitative-unweighted meta-analysis and qualitative analysis test.

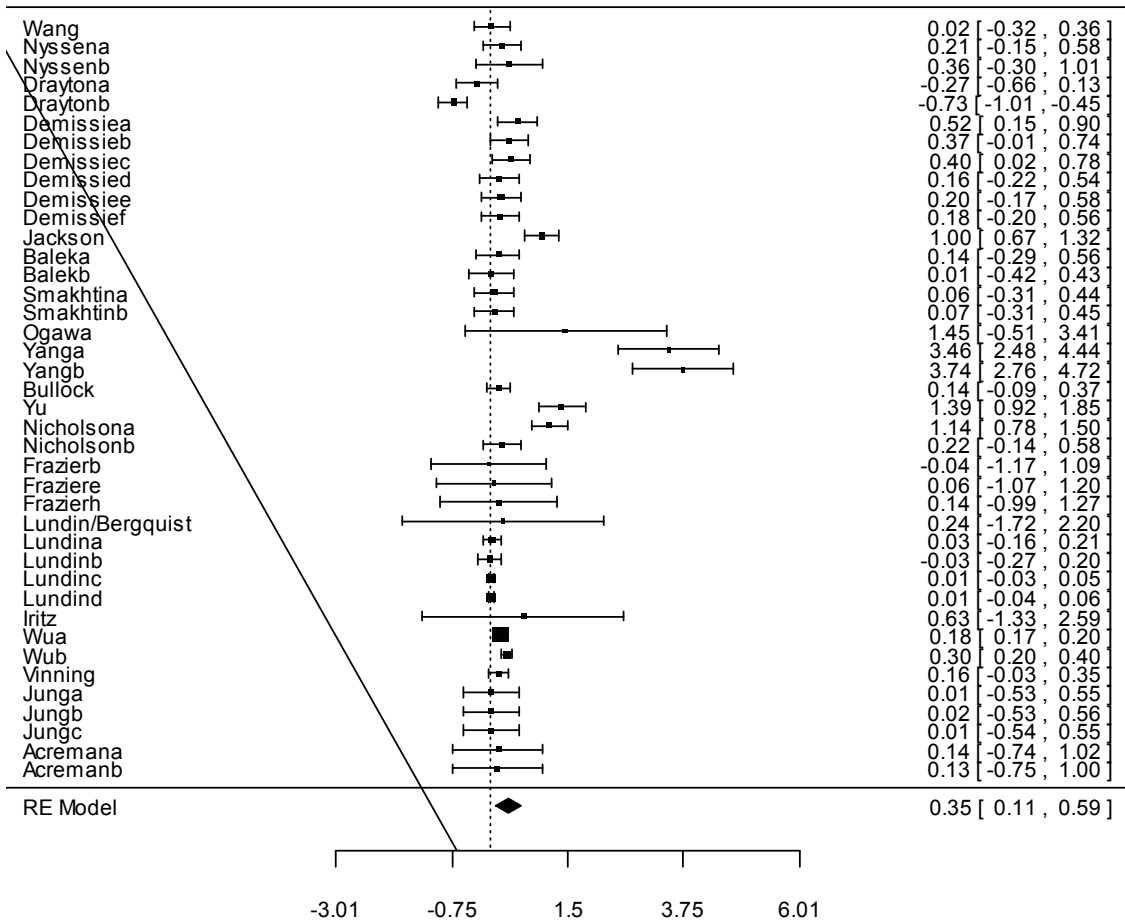


Figure 2.2. Forest plot showing Fisher's  $r$  to  $z$  transformed correlation coefficient effect sizes and summary effect (and associated confidence intervals) based on a fitted random effects model.

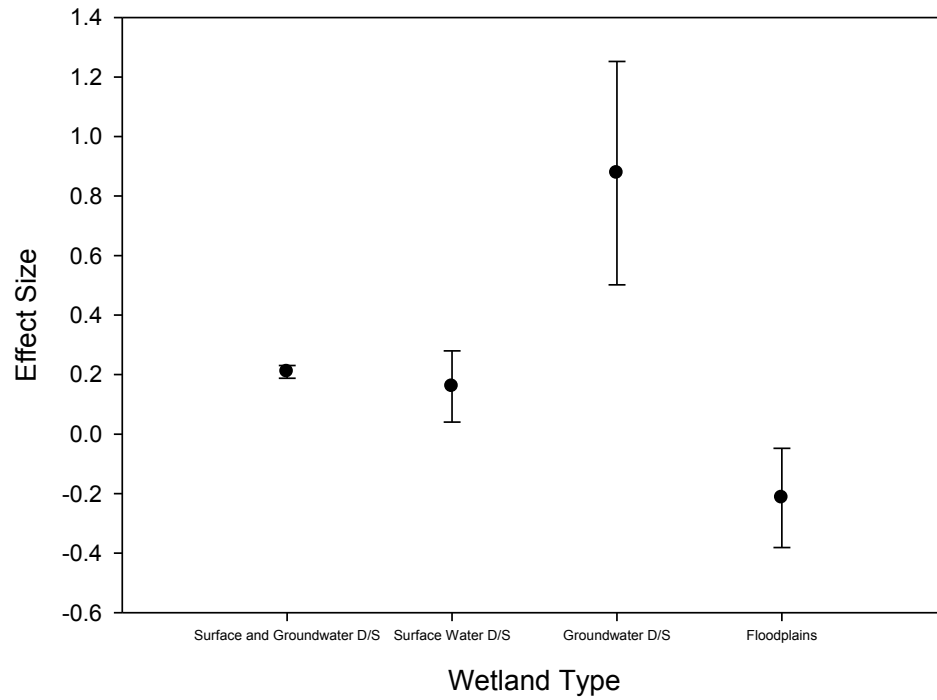


Figure 2.3. Scatterplot showing mean effect size (and associated SE) for each level of wetland type (Surface and Groundwater Depression/Slope n=9, Surface Water Depression/Slope n=11, Groundwater Depression/Slope n=12, and Floodplains n=8).

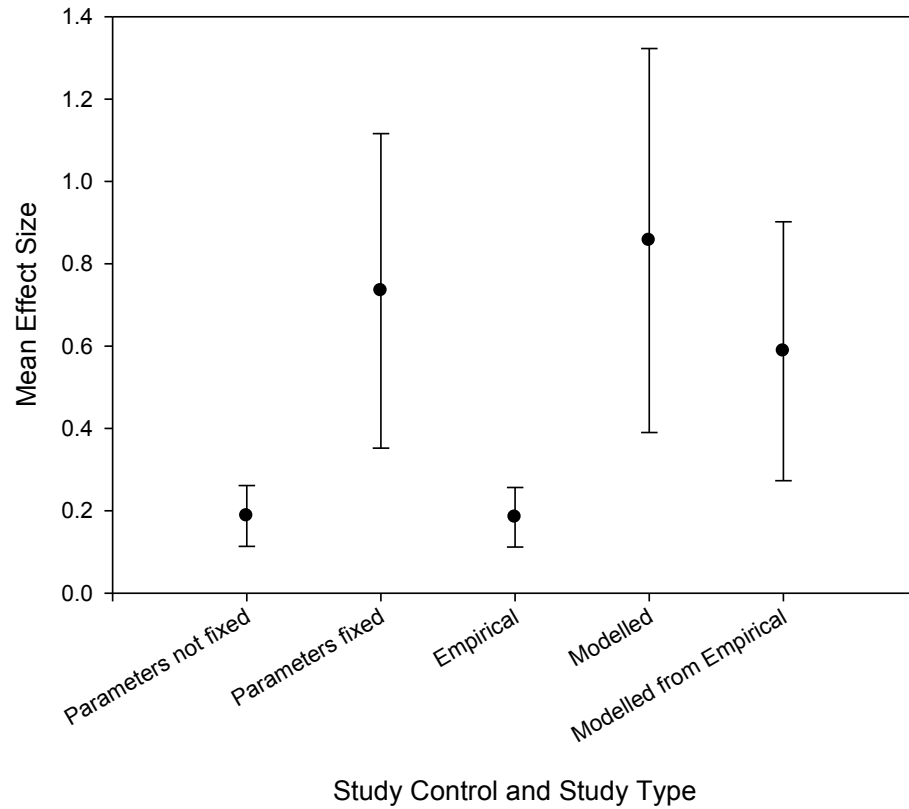


Figure 2.4. Scatterplot showing mean effect size (and associated SE) for each level of study control (parameters not fixed  $n=28$ , or fixed  $n=12$ ) and study type (empirical  $n=25$ , modelled  $n=10$ , or modelled from empirical  $n=5$ ).

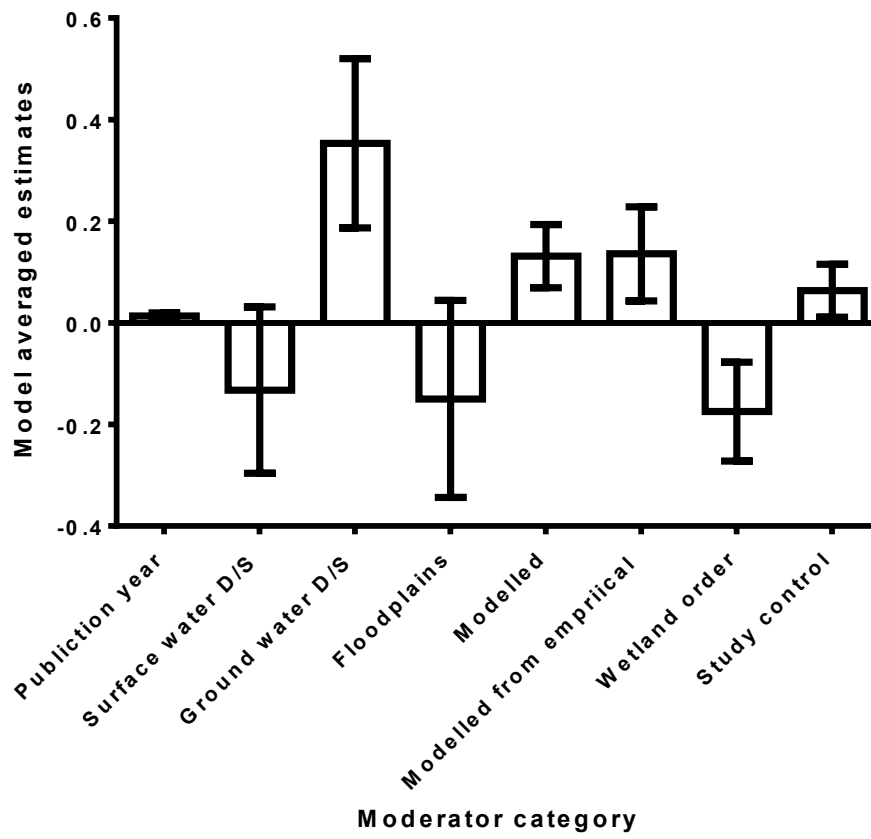


Figure 2.5. Model averaged coefficients (based on 13 models having some support) and associated standard errors) for each category of flood control moderator.

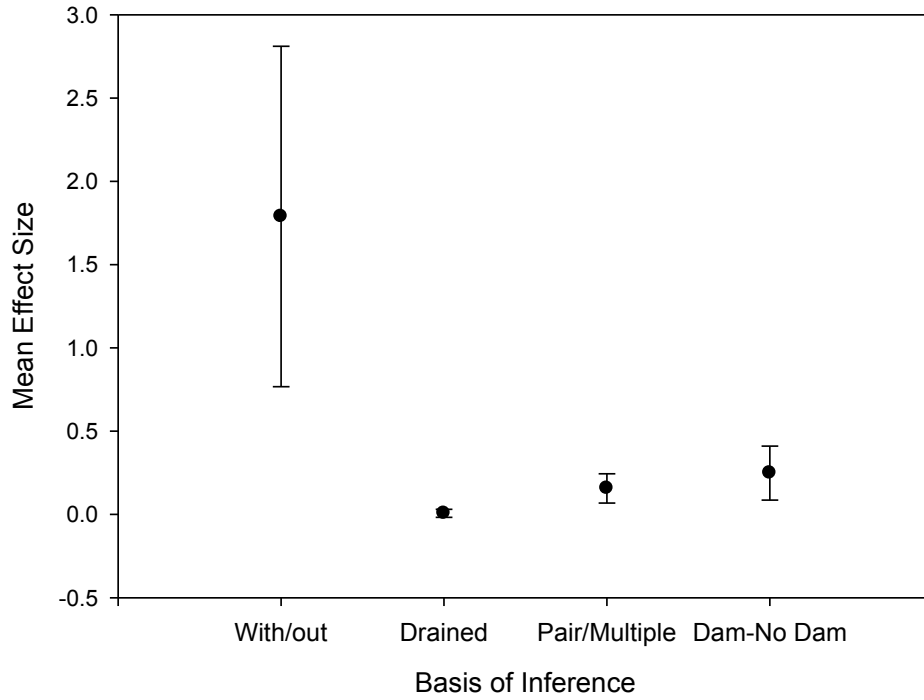


Figure 2.6. Scatterplot showing mean effect size (and associated SE) for each level of basis of inference (With/out  $n=4$ , Drained  $n=4$ , Pair/Multiple  $n=20$ , Dam-No Dam  $n=2$ ).

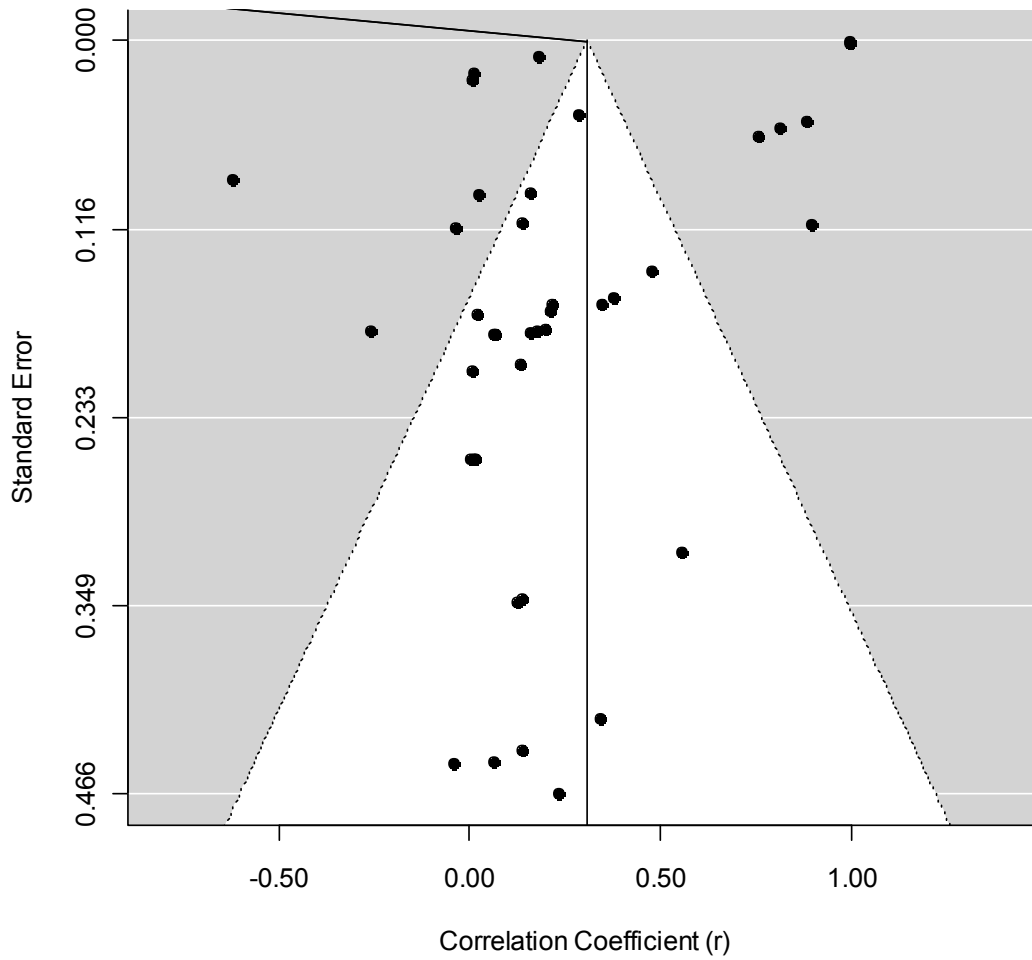


Figure 2.7. Funnel plot of effect size (Fisher's Z transformed correlation coefficient) versus the standard error of the estimate.

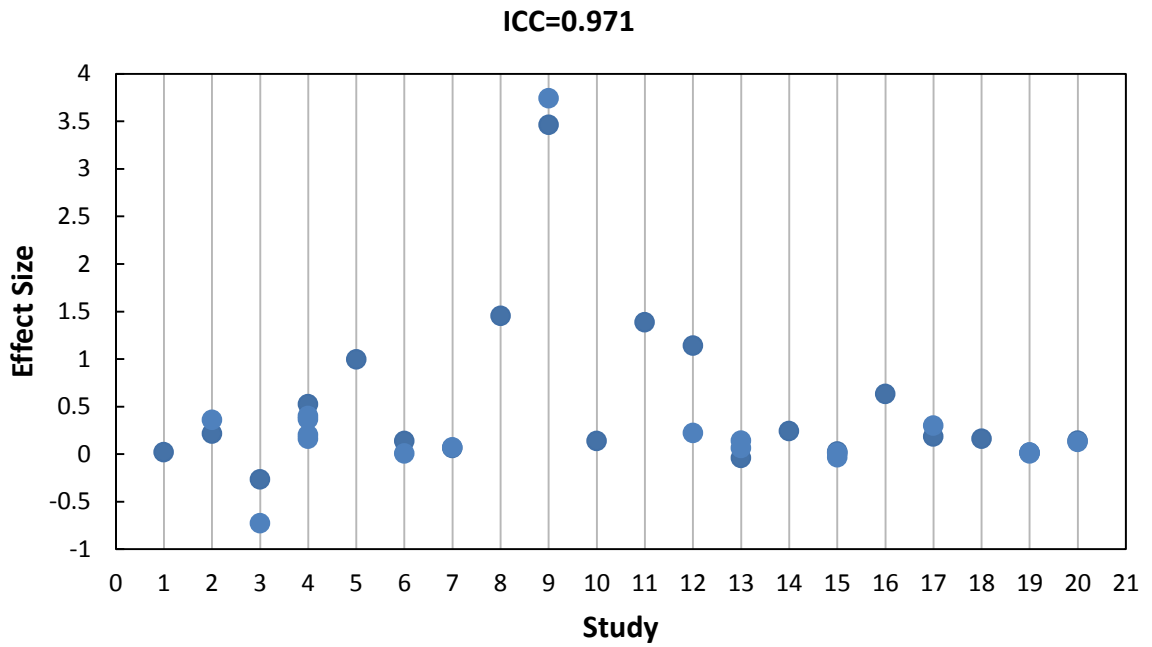


Figure 2.8. Dot plot of estimated effect sizes for individual studies included in the analysis. Studies having multiple effect sizes (as estimated for different endpoints) show a strong intra-class correlation.

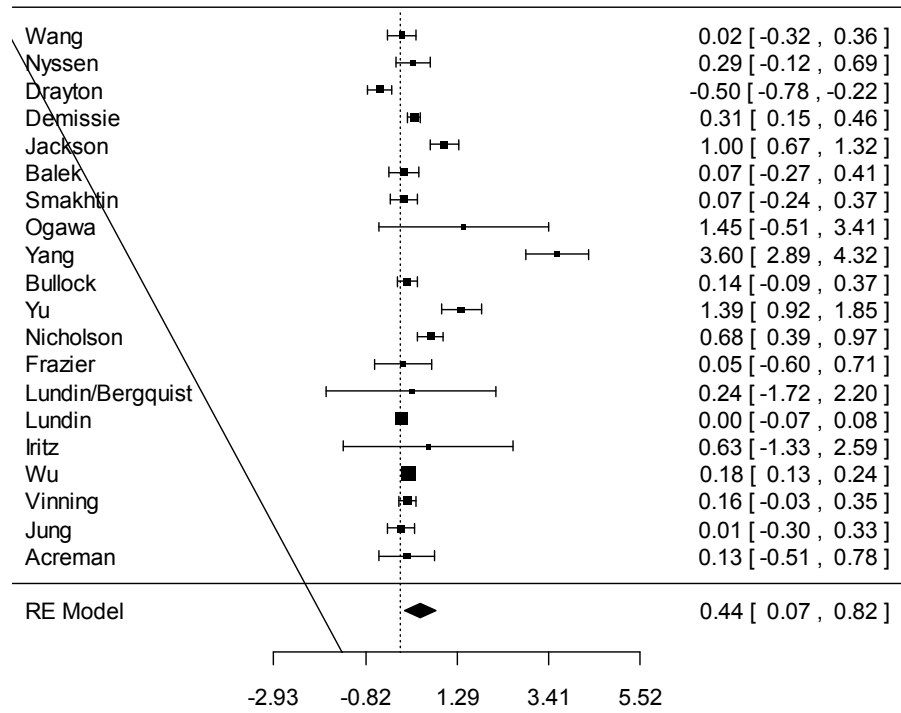


Figure 2.9. Forest plot showing  $r$  to Fisher's  $z$  transformed correlation coefficient (and associated confidence intervals) based on estimated synthetic effect sizes at the study level under a random effects model.

## **CHAPTER 3. POLLINATION SERVICE PROVISIONING BY POLLINATOR POPULATIONS IN AGROECOSYSTEMS**

### **Abstract**

The productivity of both natural and managed ecosystems depends in part upon the pollination services provided by pollinator populations. If the pollination services provided by natural pollinator populations are substantial, documented pollinator population declines may have substantial negative impacts on agroecosystem productivity. Estimating the potential impacts of declines in pollinator populations requires that we be able to estimate the level of pollination services delivered by pollinator populations in agroecosystems. On the basis of a comprehensive meta-analysis of the published literature, I find that that, on average and consistent with conventional wisdom, there is a consistent and comparatively strong association between pollinator abundance and agroecosystem productivity as inferred from measures of plant fertilization success. Metaregression analysis indicates, however, that our current ability to estimate the effect size of pollinator abundance on plant fertilization success is comparatively poor. This, combined with the observed large inter-study heterogeneity in effect sizes, means that predictions about the current level of pollination services delivered by pollinator populations in particular agroecosystems, as well as predictions about how the level of such services will change with reduced (or enhanced) pollinator population abundance, will have large uncertainty. Such uncertainty should be explicitly incorporated into estimates of both the current economic value of pollination services delivered by pollinator populations in agroecosystems, as well as estimates of how this value is likely to change under alternative management scenarios.

## Introduction

Pollination is a fundamentally important ecosystem function, both ecologically and economically. Unsurprisingly then, estimation of the economic value of pollination services delivered by ecosystems is an active area of research (Ricketts et al. 2004, Losey and Vaughan 2006). While the majority of pollination studies focus namely on insects, vertebrate pollinators are also service providers (Whelan et al. 2008, Kunz et al. 2011).

A recent assessment of the economic value of pollination services provided by insects worldwide amounted to €153 billion, representing about 9.5% of the total economic value of global agricultural production output in 2005 (Gallai et al. 2009), with a dramatic difference in the value of a ton of crops that do not depend on insect pollination (average €151) compared to those that are pollinator dependent (average €761). In a more local study, the contribution of non-native honey bees as well as native bee species to coffee production in two forest fragments (46 and 111 hectares) in a Costa Rican farm translated into \$60,000 (U.S.) per year (Ricketts et al. 2004). Unlike some ecosystem services, the economic valuation of pollination services can be estimated using replacement cost (Allsopp et al. 2008), i.e. the costs that would be required if human labourers provided the service.

In light of the estimated economic value of pollination services, the state of both managed and natural populations of pollinators is of considerable concern, both ecologically and economically. Recent losses of honeybee colonies in North America have left us with fewer managed pollinators than at any time in the last 50 years (Allen-Wardell et al. 1998), and there is good evidence that natural pollinator populations are showing similar declines (Millennium Ecosystem Assessment 2005a, Potts et al. 2010). Declines of wild pollinators and pollinator-dependent plants have, unsurprisingly, raised alarms over the loss of pollination services in agroecosystems (Keitt 2009). Although rarely detrimental to plants' ability to produce or set fruit (Free and Williams 1976, Millennium Ecosystem Assessment 2005a), decline in pollinator abundance increases the risk of reduced seed set and/or reductions in fruit or seed viability (Millennium Ecosystem Assessment 2005a), and

have been implicated in the loss of the reproductive viability of some rare plants (Spira 2001, Roels and Kelly 2011, Weston et al. 2012). Future pollinator declines seem likely given forecasts of increasing land-use change (Winfree et al. 2009), declines potentially compounded by changes in climate (Giannini et al. 2012) and habitat fragmentation, increased use of pesticides and herbicides, and invasions of non-native plants and animals (Kearns et al. 1998).

For many agricultural crops, yield depends on natural pollination and hence, the abundance of natural and/or managed pollinator populations (Free and Williams 1976, Kremen et al. 2007). Evaluation of *Annona* spp. hybrids in subtropical Australia found natural fruit set to increase linearly with the abundance of nitidulid beetles (George et al. 1989). In St Vincent, West Indies passionfruit pollination is critically dependent upon bees and hummingbirds (Corbet and Willmer 1980). Investigation of fruit production in Mexican coffee plantations found fruit production to be positively related with the richness and diversity of pollinator species (Vergara and Badano 2009). These investigations of local impacts of pollinators on agricultural production have been augmented by broader analyses. For example, Klein et al. (2007) found that of 107 crop species examined, natural and/or managed pollinators are essential for production of 13 crops, production is highly pollinator- dependent for 30 crops, moderately dependent for 27 crops, slightly dependent for 21 crops, and of unknown significance for the remaining species.

All economic valuations of ecosystem services begin with the premise that an ecosystem in a given state delivers – or is capable of sustaining – a given level of service. The task is then to estimate the marginal or total value of the service so provided. But the accuracy and/or precision (or both) of such an estimate depends not simply on the methods employed to estimate economic value, but on the accuracy of the initial estimate of the level of service currently delivered or capable of being sustained. So the obvious question arises: to what extent can we estimate the level of a given service provided by a given ecosystem in a given state? Indeed, because economic valuations are supposed to inform ecosystem management, the question is not simply the level of service the system provides in its current state, but also the extent to which changes in state affect changes in service.

In other words, the practical value of any economic valuation – irrespective of the method employed to obtain same – is linked directly to our ability to predict: (1) the current level of service provided by the ecosystem in question; and (2) how this level will change in response to changes in ecosystem state arising from different management regimes or decisions.

Here I address this question specifically in the context of a defined ecosystem type (agroecosystems) and a defined ecosystem service (pollination). My objective is to assess the current scientific evidence concerning the level of pollination service provided by natural pollinator populations in agroecosystems. On the basis of a comprehensive review of the published scientific literature, I address two specific questions: (1) what is the distribution of the estimated pollination service delivered by natural pollinator populations in agroecosystems; and (2) to what extent can we predict the estimated level of service from information about the state of the agroecosystem? The answer to the first question will I hope, provide useful information for ecological economists that could, in principle, allow them to bound estimates of the economic value of pollination services. The answer to the second question, on the other hand, will provide environmental scientists, managers and economists (among others) with valuable information on the uncertainty associated with any prediction about how the level of pollination service is expected to change under different management regimes or interventions.

## **Materials and Methods**

### ***Measurement indicators for pollination services***

Pollination is concerned with the movement of floral gametes, and more specifically, the movement of pollen to and from the reproductive parts of a flower, e.g. from anther to stigma. Pollination services are delivered by any agent that facilitates pollen transfer. For the purposes of this study, then, I consider pollination services to have been provided if there is:

- i) Pollen removal or dispersal, and
- ii) Pollen deposition/transfer to a reproductive part of a flower resulting in,
- iii) some indication of fertilization success- growth of fruit, seeds, flowers, pollen grains etc.

Associated with these criteria are a set of pollination measures (measurement endpoints) (Table 3.1) that have been employed as indicators of the level of pollination service.

### ***Wind pollination***

Few experimental designs for assessing the level of pollination service provided by pollinator populations exclude the effect of wind pollination (but see Willmer and Stone 1989 and other variations: Corbet and Willmer 1980, George et al. 1989, Heard et al. 1990, Freitas and Paxton 1996). The consequence is that the effect of natural pollinator populations *per se*, independent of wind, is largely unknown.

### ***Study design and effect size***

Studies on pollination services span a range of approaches and methodologies (Table 3.2). Most studies have Control-Impact (e.g. fruit set along an increasing spatial gradient of pollinator indicator(s)) or Before-After/Control-Impact designs (e.g. one treatment with pollinators, one excluding pollinators, with some measure of pollination service being

estimated before and after pollinator visits). Depending on the study design, effect sizes were estimated in one of several different ways.

- (1) In CI studies, effects sizes were estimated from the strength of the relationship between one or more pollination measurement endpoints (Table 3.1) for a set of sampling units (e.g. plots) arrayed over a spatial gradient of one or more pollination indicators (e.g. pollinator visits or pollinator abundance). In such designs, sample size was the number of sampling units (e.g. plots, transects, plants, flowers).
- (2) In BACI studies, effect sizes were calculated based on the size of the interaction – that is, the average difference between control (e.g. natural pollination) and impact (e.g. pollinator enclosure) plots in the difference between the level of pollination measurement endpoints before and after pollinator visits.

In some studies, the level of pollination was inferred based on one or more endpoints estimated for a set of sites spanning a gradient in the area or extent of an agroecosystem, with CI or BACI experiments being conducted at multiple sites. For example, Vergara & Badano (2009) investigated open versus enclosed fruit set rate and fruit retention rate at various sites in Mexican coffee plantations and estimated the strength of the relationship between fruit set rate and local pollinator species richness and diversity. For such studies, effect size was based on the correlation between (a) the estimated effect size at individual sites based on local CI or BACI designs; and (b) pollinator abundance or diversity at individual sites.

Effect sizes based on treatment means were generally associated with BACI or CI studies, most of which were exclusion studies (treatments where pollinators were excluded, with indicators of pollination and/or plant production (e.g. fruit weight or yield etc.) then being compared with plots or sites from which natural pollinators were not excluded-CI; or if plant production was estimated a time before enclosure than following enclosure-BACI).

## ***Meta-analysis***

Meta-analyses were performed as detailed by Borenstein et al. (2009) and Harrison (2011). In estimating effect sizes, I employed a random-effects model, as there is ample reason to expect that the true effect size will vary from study to study and that there is no true underlying effect size shared by all studies. Meta-regression was used as a meta-analytic tool to examine the impact of moderator variables on the dependent variable of effect size using regression based techniques. Meta-regression analyses and plots were created using the metafor package in R (Viechtbauer 2010).

Effect sizes were calculated using the standardized mean difference between groups or correlation coefficients (Table 3.2), as described above. All initial effect sizes were converted to correlation coefficients, thence to Fisher's  $z$  scale (an approximate variance-stabilizing transformation) as the principle effect size measure of interest (Borenstein et al. 2009). For presentation purposes, effect sizes have been reconverted to correlation coefficients.

## ***Meta-Regression***

I used mixed-effects meta-regression to model the effects of one or more potential predictors (moderators) (Table 3.3, for full candidate moderator description see Appendix F) on estimated effect sizes using the DerSimonian and Laird method to estimate heterogeneity (DerSimonian & Laird 1986). Candidate moderators included variables such as, for example, the study context (geographical location, duration and timing of the study, etc.), study design (e.g. Control/Impact versus Before/After-Control/Impact), or the attributes of the agroecosystem in which the study was conducted (e.g. presence of wild vegetation, type of culture, presence of managed insect colonies etc.). Fitted models were evaluated and assessed on the basis of Akaike Information Criterion (AIC),  $R^2$  analog, Deviance, Log-Likelihood, QE (residual heterogeneity) and QM (Test of moderators). Akaike's Information Criterion (AIC) scores, AIC differences and Akaike weights were calculated to select the best model (Burnham & Anderson 2002). During model selection using an information-theoretic there was no overwhelming support for any one particular

model, so model averaged estimates of candidate moderators were determined from multimodel inference (i.e. inferences based on the entire set of models)(Burnham & Anderson 2002).

On the basis of fitted meta-regression models, I estimated the predictive value of moderators, or sets thereof, with respect to observed effect sizes using individual studies as the sampling unit and analog  $R^2$  as a measure of predictive power. Heterogeneity was assessed using weighted sum of squares (Q); tau-squared ( $T^2$ ) (estimate of between studies variance); the proportion of observed variance that reflects real differences in effect size ( $I^2$ ); and ratio of total variability to sampling variability ( $H^2$ ).

To explore potential biases in the set of selected studies, I used funnel plots and fail-safe N.

### ***Multiple pollination indicators per study***

Many studies generated multiple effect sizes, one for each of several different pollination indicators. This introduces two potential problems: the (1) standard summary effect treats each effect size as an observation, thereby giving studies with multiple estimates more weight in the analysis than studies with only one estimate; and (2) the analysis ignores the possibility of within-study correlations among effect size estimates, potentially leading to an overestimated precision of the summary effect (Borenstein et al. 2009). To address this potential bias, I calculated the intra-class correlation (ICC) defined as

$$ICC = \frac{\sigma^2(b)}{\sigma^2(b) + \sigma^2(w)} [Eq. 1]$$

where  $\sigma^2(w)$  is the pooled variance in effect sizes within studies, and  $\sigma^2(b)$  is the between study variance.

I then calculated a 'synthetic effect size' which is a summary effect defined as the mean effect size in that study based for all estimated pollination indicators estimated as well as a synthetic within-study variance based on the intraclass correlation using Eq. 5 of Borenstein et al. (2009, p. 228).

Using the DerSimonian and Laird method to estimate heterogeneity (DerSimonian and Laird 1986), once again meta-regression models were fitted to the data to examine the impact of candidate moderators on synthetic effect size.

### ***Study retrieval***

Literature searches were conducted in ISI Web of Science from May –November 2012. Search keywords included Field 1: “pollination”, “seed production”, OR “seed movement”. These keywords were searched in conjunction with Field 2 (ecosystem type): “agroecosystem\*”, “agro-ecosystem\*” OR “cropland\*” (**A in Figure 3.1**). Additional studies were retrieved and reviewed by locating articles referenced by a previously retrieved article as well as reviewing published works of authors that appeared (on the basis of title and abstract of the article) to pertain to pollination services delivered in agroecosystems (**B in Figure 3.1**).

### ***Inclusion criteria***

Included studies (I) report estimates of at least one pollination indicator relating to pollination from the set of endpoints shown in Table 3.1, and at least one potential pollination moderators (Table 3.3), estimated or measured on a set of sampling units (e.g. experimental replicates, sites, etc.); (ii) provide sufficient statistical information (mean, standard deviation or some estimate of precision, correlation, sum of squares, sample size for the various groups, etc.) such that effect sizes could be estimated; (iii) were published in a peer-reviewed scientific journal or a publication (e.g. book or review) that contained a set of peer-reviewed entries; and (iv) reported results from agroecosystems (i.e. at least some sampling sites were located in or adjacent to areas where agriculture was the dominant land use). Initial screening involved reading abstracts of all retrieved articles and eliminating those that, on the basis of information provided in the abstract, did not meet the four inclusion criteria (**92 studies, C-Figure 3.1**).

Forty-five of the 84 retrieved studies did not meet the inclusion criteria and were excluded because of inadequate study design or insufficient statistical data to estimate effect sizes (**45 studies, D-Figure 3.1**):

In eleven instances, authors were contacted for the missing information, only two of which were answered successfully. Of these studies excluded from the quantitative meta-analysis because of insufficient information required to estimate effect sizes 11 were included in a separate qualitative analysis.

### ***Qualitative analysis test***

For some studies, insufficient information was provided that would permit estimates of effect size. For these studies, I employed a variant of the more usual vote-counting (Harrison 2011) method. Instead of classifying studies on the basis of significant or non-significant type I error rates, I used the author's own statements about the significance of their results. An author statement which, in my view, would be interpreted as providing evidence that pollinator populations positively contributed to agricultural productivity, was given a positive score (+1). By contrast, an author statement which, in my view, would be interpreted as providing evidence that pollinator populations did not contribute to agricultural productivity, was given a negative (-1) score. I then used a sign test to test the null hypothesis of an equal distribution of negative and positive scores (Borenstein et al. 2009). Studies were assigned a value of +1 only if it was clearly stated that a positive effect was detected. If the effect was negligible or non-existent by the author's own account, it was given a -1 score. Only one score was assigned per study. Studies that had multiple outcome statements in conflicting directions were not included in the qualitative analysis.

## Results

In total, 192 effect sizes were calculated from 39 studies encompassing 9 animal orders and 57 families, based on 32 distinct crop species.

The weighted meta-analysis yielded a high positive weighted overall mean effect size ( $0.72 \pm 0.08$  (1 SE),  $N = 192$ , 95% CI = [0.56, 0.88],  $p = <0.0001$ ; Figure 3.2), corresponding to an overall mean effect size correlation of 0.62 (95% CI = [0.52, 0.70]). Five different measures of heterogeneity all indicated substantial variation in effect size among studies in the sample ( $Q = 8750$ ,  $df = 191$ ,  $p < 0.001$ ;  $T^2 = 1.19$ ;  $T$  (estimated standard deviation of true effects) = 1.09;  $I^2 = 97.8\%$ ;  $H^2 = 46.0$ ).

### ***Mixed Effects Models***

A subset of  $k=173$  effect sizes and associated moderators was established from the full set of 192 effect sizes eliminating those effect sizes (and associated studies) that were missing information on moderators of particular interest including : the type of *agriculture* (*i.e.* mono versus poly culture) (Singh 1989-4, Freitas & Paxton 1996), whether the crop was commercial or subsistence, and whether the crop fruited or produced a nut) (Mänd et al. 2002-2, Morandin & Winston 2005-2, Morandin & Winston 2006, Albrecht et al. 2007); or whether implicated pollinator species were social or solitary (Willmer & Stone 1989). Four effect sizes were eliminated from the analysis because sample size for indicators was considered too small to yield reliable results).

For this subset, twenty one moderators showed informative bivariate associations with effect size (Table 3.4). For complete model results see Appendix G.

On the basis of the original examination of the bivariate effects of individual candidate moderators, I defined a set of 101 candidate models involving linear combinations of the top eight moderators (based on reduction in AICc relative to the base model) shown in Table 3.4, constrained by the requirement that, for any fitted model, the number of estimated parameters was fewer than 14, including the intercept. This condition was imposed to ensure that the ratio of sample size to the number of candidate moderators was around 10, sufficient – at least in principle – to ensure reasonable model stability and/or

sufficient precision of estimated coefficients (Vittinghoff et al. 2005, p. 149). Of these 101, fifteen had  $\Delta$  AICs  $< 7$  (Table 3.5), with the overall best model including the measurement endpoint employed to assess the level of pollination service delivered (*pollination measurement indicator*), the indicator used to characterize the pollinator community (*pollinator community attribute*), the type of pollination method employed by natural pollinator populations when collecting or transferring pollen (*buzz pollination*) and the *year of publication* (Table 3.5). As there was no overwhelming support for any one model (Table 3.5), estimated coefficients were based on model averaging (Figures 3.3, 3.4, 3.5).

A second sub sample of effect sizes ( $k = 112$ ) was defined to include studies that reported estimates of two additional moderators: the number of pollinator species (as an index of pollinator community diversity) and the total number of pollinator visits over the sampling period (as a measure of overall pollinator abundance). For this sub-sample, thirteen moderators (Table 3.6), including the number of pollinator visits, showed informative bivariate associations with estimated effect size. For full model results, see appendix H.

### ***Qualitative analysis test***

Of the 11 studies included in the qualitative meta-analysis, all 11 indicated a positive effect (two-tailed sign test,  $p < 0.0001$  – see Borenstein et al. (2009)) of pollinators.

### ***Publication Bias***

Visual inspection of the funnel plot (Figure 3.6) of the standard error of the estimate versus z-transformed effect size suggest little bias of the type such plots are supposed to uncover (see Borenstein et al. 2009) but substantial heterogeneity in effect size. A formal test for funnel plot asymmetry based on the random-effect regression test also suggested little asymmetry ( $z=0.82$ ,  $p=0.41$  and, one presumes, little publication bias). However, one should interpret these results cautiously; regression tests for asymmetry have comparatively low power (Borenstein et al. 2009).

Using Duval and Tweedie's Trim and Fill approach (2000a, 2000b) the estimated number of missing studies on the left side of the funnel plot is zero. Hence, my estimate of the effect size and the estimate of an unbiased effect size as calculated by Duval and Tweedie's Trim and Fill approach are very similar, such that no further augmentation was required to render the funnel plot more symmetric.

### ***Fail-Safe N***

Rosenberg's (2005) Fail-Safe N (331222; observed significance level < 0.0001, target significance level = 0.05), as well as Rosenthal's (1979) Fail-safe N (230191 - Observed Significance Level: <0.0001, Target Significance Level: 0.05) both suggest that the impact of bias is small.

### ***Multiple effect sizes per study***

Based on a synthetic effect size using the correlation among outcomes within studies (Table 3.7), the weighted meta-analysis increased to  $1.01 \pm 0.14$  (1 SE),  $N = 39$ ,  $p < 0.0001$  (95% CI = [0.74, 1.29] (Figure 3.7), corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.77 (95% CI, [0.59, 0.87]).

Treating synthetic effect sizes as the dependent variable, I investigated the association with several candidate moderators at the study level ( $k=39$ ) (Table 3.8). Of 16 predictor moderators investigated, only four (culture type, pesticide use, mixed, and exclusion effect) showed a bivariate association with synthetic effect size. With the exception of exclusion effect, all three of these predictor moderators also showed bivariate associations with the larger sample of effect sizes (see Table 3.4). This suggests that for these variables at least, the inclusion of multiple effect sizes per study is not introducing any significant bias.

## Discussion

My meta-analysis of the published literature provides compelling evidence that, overall, the pollination services provided by natural pollinator populations in agroecosystems are substantial. My analysis indicates that, overall, a greater level of pollination services was provided in monoculture versus polyculture agroecosystems, and in agroecosystems without natural vegetation compared to those with natural vegetation. Greater provisioning was also associated with the presence of managed pollinator colonies; buzz pollination; with the level of service delivery being inferred from pollen efficiency/deposition as an indicator rather than fruit set, fruit weight, pollen grains, seed mass and seed set; and with more diverse (in terms of both abundance and richness) pollinator communities. However, despite informative associations with a number of moderators, overall predictive power of even the best model was comparatively modest, with most (about 60%) of the variation in estimated effect sizes remaining unexplained.

My results provide compelling evidence that the inferred level of service (i.e. effect size) provided by natural pollinator populations in agroecosystems varies depending on which indicators are used to characterize the level of service provisioning. The greatest effect was observed for pollen efficiency and deposition, indicators that are intimately related to pollinator abundance and activity (Kunin 1993, Greenleaf & Kremen 2006), and which are less likely to be affected by factors other than pollinator abundance/activity. By contrast, indicators such as fruit weight, seed set and seed mass showed considerably smaller effect sizes. Such indicators are more likely to be influenced by environmental conditions largely independent of pollinator abundance or activity, including fertilizer use (Wallace & O'Dowd 1989, Oloyede et al. 2013), flowering time (Sabat & Ackerman 1996), soil moisture (George & Nissen 1988) and weather conditions during the growing season (Prasad et al. 2000, Hedhly et al. 2007), as well as fruit or seed losses caused by disease (Nadel & Pena 1994).

Studies reporting buzz pollination also showed, on average, a greater level of inferred pollination service. Buzz pollination is used by certain bees to release pollen, resulting in enhanced pollination efficiency (Buchmann 1983, Thorp 2000). Certain flowers

(e.g. *Pedicularis* spp., *Melastomataceae* spp. (Larson & Barrett 1999)) depend on buzz pollination and there is, moreover, evidence that buzz pollination improves the chances of cross-pollination upon multiple visits if pollinator visitation is frequent (Kawai & Kudo 2009).

My analysis also suggests that that the level of pollination services delivered by pollinators is more strongly related to Shannon diversity of the pollinator community than to richness or abundance considered separately. In a recent review of the effect of diversity on pollination, Cardinale et al. (2012, Table 1) suggested that although a positive relationship between diversity and pollination services is predicted, empirical results are mixed. For example, while most studies included in my analysis showed a positive relationship with the inferred level of pollination services, Badano & Vergara (2011) showed that fruit set decreased with increasing honey bee abundance. Although most studies which investigated the effect of species richness reported a positive relationship with pollination services, this relationship was generally weak (e.g. Albrecht et al. (2007)).

The stronger association with Shannon diversity may in part reflect methodological bias. Reported richness was invariably based on all species observed during pollination surveys, unless a species was explicitly identified as not contributing to pollination. As the contribution of each species to pollination of target crops is largely unknown, it is entirely possible that some – perhaps many – of the enumerated species made negligible contributions. Others have also suggested that abundance may be more important for pollination provisioning than species richness (e.g. Faye 2013).

My analysis also indicates that although natural (wild/native) pollinators provide substantial pollination services, agroecosystems with managed hives/colonies showed a greater average level of pollination services than those without. While there is some evidence that natural pollinator populations provide sufficient (fruit and seed viability) or superior pollination to managed honey bees (Javorek et al. 2002, Greenleaf & Kremen 2006, Badano & Vergara 2011), other authors reported pollination by honeybees to be an improvement over natural pollinators (Free & Williams 1976, Ewies & El-Sahhar 1977, Heard et al. 1990, Freitas & Paxton 1996). This result is likely clarified by studies which

incorporate managed hives/colonies surely increase pollinator abundance thus are likely to show higher levels of pollination service adding to what is already provided by natural pollinator populations.

My results further suggest that monoculture agroecosystems with little natural vegetation show, on average, greater pollination services by pollinator populations than those with intercropped natural vegetation. There is considerable evidence that natural patches in agroecosystems enhance pollination services and crop yield (Morandin & Winston 2006, Ricketts et al. 2008). While the effect of distance and location of natural habitat/patches was not quantified in this analysis because data were too sparse to include comprehensively, I was able to examine if whether natural vegetation inclusion in agroecosystem crop systems affected pollination services. Common sense suggests the abundance of (natural) pollinators would increase with the presence of natural vegetation. However, network analysis suggests that plant-pollinator interactions display a high level of complementary specialization (Blüthgen & Klein 2011). My results may suggest, (natural) pollinators may be concentrating less on target crop species when more natural vegetation is present. Thus, the benefits (in terms of agricultural productivity) of increased abundance due to natural vegetation may be outweighed by the cost of pollinators concentrating more on natural plants. To this point, pollinators may show density-dependent preferences such as neophobia (an avoidance of unfamiliar items), and there is some evidence that increasing wild flower abundance may shift foraging preferences away from monoculture agrocrops (Rands & Whitney 2010). Thus, within a monoculture, a larger proportion of the pollinators may well be involved in agroecosystem pollination whereas in systems with intercropped natural vegetation, pollinators may be attracted to natural plant species compared to crop target species.

Consistent with expectations, the number of individual visits by animal pollinators showed a positive association with the level of pollination services delivered. Regardless of the diversity of pollinators, one would expect pollination success to increase with the number of visits as long as visitors were actually pollinating rather than nectar robbing (Malooof & Inouye 2000). Many studies provide evidence of a positive correlation between

the pollinator visitation rates and pollination success (Mänd et al. 2002, Klein et al. 2003a, and b, Winfree et al. 2007, Badano & Vergara 2011, Vilhena et al. 2012).

### ***Sources of uncertainty***

*Study retrieval.* A discouragingly large proportion (26%) of candidate studies were missing information required to calculate effect sizes. On the other hand, estimates of fail-safe N are large (e.g. 230191-331222) suggesting (to the extent that one can rely on such estimates – see, for example, Scargle 2000) that exclusion of such studies is not expected to have a substantial impact on my results.

*Characterization of moderator variables.* Studies on the effect of pollinator populations on pollination services in agroecosystems not only show extensive variation in sampling methods and intensity and experimental design, but also in the extent to which (and the type of) information provided on candidate moderators. Some candidate moderators (e.g. whether the agrocrop in question was a monoculture or polyculture; or whether shade was included as a factor in study design or not) were comparatively easy to score for a given study, as this information was invariably reported and possible levels were clear and unambiguous. For other candidate moderators (e.g. whether pesticide was applied) the information required to correctly score a particular study was much less systematically reported, making scoring considerably more ambiguous, thereby increasing what amounts to measurement error. It is, therefore, entirely possible that the failure to detect effects of some candidate moderators merely reflects this greater measurement error. Such measurement error will also influence the fit of even the best models.

### ***Implications***

My results have several implications. First, I have shown a consistent positive effect of pollinators on the level of pollination services delivered to agroecosystems. I have also shown that, on average, greater levels are associated with greater diversity of pollinator communities. There is, therefore, reasonably strong evidence that declines in wild and managed pollinator diversity and abundance is very likely to have a negative effect on

productivity of agroecosystems. Maintaining agroecosystem productivity will then depend on either reversing the decline in pollinator populations, or adopting appropriate – but almost certainly more costly - compensation strategies (Losey & Vaughan 2006, Allsopp et al. 2008).

*Second*, my results indicate that detected associations with several moderators notwithstanding, the predictive power of even the best models is modest at best. This, combined with the observed heterogeneity of effect sizes, means that, in the absence of considerably more detailed *in situ* information about the specific agroecosystem(s) of interest, including the endogenous pollinator community, any estimate of the current level of pollination delivered by a natural pollinator populations; or the expected change in service provisioning under alternative management actions, will have a large associated uncertainty.

Ecological economists already have a deep appreciation of the value of pollination services (Allsopp et al. 2008, Gallai et al. 2009). But the estimated economic value of these services is highly variable (Losey & Vaughan 2006, Allsopp et al. 2008, Hein 2009), depending on a number of factors including method used (Allsopp et al. 2008, Kasina et al. 2009), as well as the availability of alternative pollinators, costs related to switching to alternative crops and whether pollinator loss will affect one crop or a multitude of crops (Hein 2009). From an agricultural standpoint, valuation of pollination services is made more complex by determining the proportions that could be attributed to native, as opposed to managed, pollinators, will vary widely for each crop depending on geographic location, availability of natural habitat, and use of pesticides (Kremen 2002). Furthermore economic estimates make assumptions on markets having an infinite elasticity of demand which is economically unrealistic given that consumers are unlikely willing to pay the same for agricultural productivity when supply is abundant versus when it is scarce (Gill 1991). To this variability (and hence, associated uncertainty) must now be added the constraint that in the absence of detailed system and location-specific information, our current ability to predict the level of pollination services provided by pollinator populations, is low. Hence, any estimate of the economic value of pollination services delivered by pollinator

populations in agroecosystems will have large, even very large, uncertainty – essentially, the combination of (a) uncertainty in estimated value for a given level of service; and (b) uncertainty in the level of service provided. Moreover, substantially reducing the former uncertainty will require considerably more detailed scientific knowledge about the specific system under consideration.

This conclusion has potential implications to the implementation of market-based instruments (MBIs) for conserving pollinator communities or, more generally, for the payment for pollination (or any other) services. All existing MBIs and payment schemes which, in principle, could help conserve ecosystem services require that (a) the current level of service be estimated; and (b) that future provisioning under different management actions or scenarios be predicted. For example, Kremen et al. (2004) showed that in northern California, pollination service provisioning by native bees was positively correlated with the amount of natural upland habitat within 2.4 km of watermelon farms. This relationship offers the potential for landowners of natural habitat to auction the (natural) pollination services associated therewith to surrounding farmers. In such a scheme, bids would be based on the expected level of service delivered per unit area of natural habitat, as well as the uncertainty associated with such estimates. For several types of auctions, uncertainty both prolongs bidding and decreases the expected selling price (Raviv 2009). As such, the enthusiasm of landowners for selling, and of farmers for purchasing, will be influenced by uncertainty in the estimated level of pollination provisioning.

More generally, the attractions of payment schemes notwithstanding, lack of scientific knowledge about service provisioning– that is, scientific uncertainty and lack of predictability - constitute significant barriers to their implementation (Daily and Matson 2008, Engel et al. 2008, Daily et al. 2009). For example, scientific uncertainty in the provisioning of ecosystem services (as well as the valuation of any such services provided) renders the assessment of tradeoffs associated with alternative land use practices considerably more complicated (Johnson et al. 2012). While my results do not, of themselves, immediately eliminate payments for ecosystem services as a feasible approach to environmental conservation, they suggest that in developing and implementing any such

approach, both proponents and critics should adopt the epistemologically pragmatic predisposition that:

- (1) Given a particular ecosystem (or set thereof) and service (or set thereof), environmental science may be able to provide some rough estimate of the level of service currently provided if the associated ecological function(s) are few and well characterized, and we can agree on what endpoints ought properly be employed to characterize these functions (see, e.g. Liss et al. 2013);
- (2) Given a set of alternative management actions, environmental science may be able to provide semi-quantitative ranking of the effect on those ecological services satisfying the criteria in (1) above, if the relationship between management action and the levels of associated ecological functions is well characterized. If these conditions are not satisfied, then an ordinal ranking is likely the best one can do with any degree of confidence and credibility.
- (3) If the enthusiasm (by buyers and/or sellers) for payment schemes depends upon greater certainty associated with estimates of service provisioning, then, in the absence of marked enthusiasm (and resources) for more detailed scientific research, alternate strategies – perhaps of the command and control variety – may be the more realistic alternative.

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## Tables

Table 3.1. Potential pollination service indicators, associated definitions and example studies in which the level of pollination service was inferred from the indicator in question.

| <i>Pollination indicator</i>    | <i>Definition</i>   | <i>Reference</i>                     |
|---------------------------------|---|--------------------------------------|
| <b>FRUIT</b>                    |   |                                      |
| Number of fruit                 | Number of mature fruits per branch/flower/plant etc.  | Singh (1989)                         |
| Fruit set (Number of fruits)    | The proportion of floral ovaries that develop into mature fruit per branch/ flower bud/plant etc.   | Klein (2009)                         |
| Fruit retention                 | The proportion of initiated fruits per branch that reach maturity. Averaged over a sample of branches, this indicator may also be used at the plantation scale.   | Badano and Vergara (2011)            |
| Fruit set rate difference       | The difference between the fruit set rate obtained from open (open to wind and animal pollination) and self-pollination (closed) treatments. Averaged over a sample of branches, this indicator may also be used at the plantation scale. | Badano and Vergara (2011)            |
| Fruit retention rate difference | The differences between the fruit retention rate obtained from open and self-pollination treatments. Averaged over a sample of branches, this indicator may also be used at the plantation scale.   | Badano and Vergara (2011)            |
| Fruit weight/mass               | Quantitative measure of the weight or mass of fruit(s) per sampling unit (branch/flower/plant)  | Philpott et al. (2006)               |
| Fruit yield                     | The total fruit production per unit area (e.g. kg/ha)   | Veddeler et al. (2008)               |
| Number of flower buds           | Number of undeveloped embryonic flower shoots per branch  | Philpott et al. (2006)               |
| Fertilization rate              | The number of visits by pollinators per flower required to achieve fruit maturation.  | Philpott et al. (2006)               |
| <b>SEEDS</b>                    |   |                                      |
| Seed set                        | Number of ovules that successfully develop into seeds per sampling unit (fruit, plant)  | Ewies and El-Sahhar (1977)           |
| Seed mass/weight                | The weight or mass of seed(s) per sampling unit (fruit, plant)  | Albrecht et al. (2007)               |
| Seed/Pollination deficit        | The average difference in seed set between open pollinated and supplementary (hand) pollinated flowers  | Morandin and Winston (2005)          |
| Number of seeds per fruit/plant | The number of seeds per fruit or per plant  | Steffan-Dewenter and Tschardt (1999) |
| <b>POLLEN</b>                   |   |                                      |
| Pollen grains per flower/stigma | Number of pollen grains per individual stigma or flower or proportion of pollen grains germinated per individual stigma or flower   | Morandin et al. (2001)               |
| Pollination efficiency          | Number of seeds resulting from individual (pollinator) visit  | Greenleaf and Kremen (2006)          |
| Pollen deposition               | Number of pollen grains deposited per individual (pollinator) visit   | Javorek et al. (2002)                |
| <b>FLOWERS</b>                  |   |                                      |
| Number of flowers               | Number or flowers per sampling unit (inflorescence, panicle, raceme)  | Mand et al. 2002                     |
| Number of flower buds           | Number or flower buds per sampling unit (inflorescence, panicle, raceme)  | Philpott et al. (2006)               |

Table 3.2. The effect size measure employed for different pollination service study designs and methods of calculating pollination effect size for different statistical estimates and study designs.

| Statistical estimate   | Study Design  | Effect size measure   | Example Reference  |
|--|---|---|--|
| Effect size based on correlation (e.g. the correlation between fruit set and the richness of pollinator communities) | Estimates can be made from Control-Impact and Before-After/Control-Impact designs | Correlation Coefficient (r) or Coefficient of Determination ( $r^2$ ) | Albrecht et al. (2007), Klein (2009), Vergara and Badano (2009). |
| Effect size based on mean difference (e.g. fruit set in a treatment excluding pollinators and including pollinators) | Estimates can be made from Control-Impact and Before-After/Control-Impact designs | Standardized mean difference  | Tepedino (1981), Raw and Free (2003), Otieno et al. (2011).      |

Table 3.3. Candidate pollination service moderators, and associated levels (for categorical moderators).

| <b>Moderator</b>          | <i>Description and levels (categorical moderators)</i>  |
|---------------------------|---|
| <b>Country</b>            | <i>Country of study</i>   |
| <b>Year</b>               | <i>The year the study was published</i>   |
| <b>Study area</b>         | <i>The total area of the study, i(including all units (e.g. sampling sites), in hectares</i>  |
| <b>N</b>                  | <i>Number of sampling units (e.g. plots, fields, transects, farms.)</i>   |
| <b>Agroecosystem type</b> | <i>The type of agroecosystem. Possible levels include: orchard, plantation, farm, greenhouse, grove (small group of trees), agro-forest (combining tree and shrub plantations and the farming of low-lying herbaceous plants)</i> |
| <b>Mixed</b>              | <i>Whether study plots included natural vegetation (score 1) or not (score = 0)</i>   |
| <b>Culture type</b>       | <i>The type of cultivation, either monoculture (“Mono”), polyculture (“Poly”), or mixed monocultures and polyculture fields (“mixed”)</i>   |
| <b>Hives</b>              | <i>Whether the study mentions the use of managed insect colonies (score=1) or not (score=0).</i>  |
| <b>N_Hives</b>            | <i>Number of hives/colonies used in the study</i>   |
| <b>Pvisit</b>             | <i>Whether pollinator visitation was measured to infer pollination services (score=1) or not (score=0).</i>   |
| <b>Exclusion</b>          | <i>Whether pollinator exclusion was employed in the study (score=1) or not (score=0)</i>  |
| <b>St_Design</b>          | <i>Whether a study was a CI (Control-Impact) or a BACI (Before-After/Control-Impact) design</i>   |
| <b>Species richness</b>   | <i>The total number of different pollinator species, on the basis of which an effect size was calculated described in the study</i>   |

|                               |  |
|-------------------------------|--|
| <b><i>N_ind/visits</i></b>    | <i>Total number of recorded individual plant visits by individual pollinators included in effect size (per effect size)</i>  |
| <b><i>Native</i></b>          | <i>Whether the study investigated pollination provided by native (unmanaged) species or by introduced or managed species. Possible levels include: native only, introduced only or both native and introduced. The proportion of pollinators that were native: mostly managed (score=0) or mostly native (score=1). Proportion is based on overall species. Although native and introduced species may be present, there can be a much larger proportion of one or the other. Whether, based on the list of provided pollinator species, the pollinator community was dominated by natural (score = 1) or managed (score = 0) species.</i> |
| <b><i>P_Native</i></b>        | <i>Whether the enumerated pollinator community included only volant pollinators, only non-volant pollinators, or both. Possible levels in the study included: both flying and non-flying pollinators, only flying, or only non-flying</i>  |
| <b><i>Flying</i></b>          | <i>Whether the enumerated pollinator community included only social pollinators, only solitary pollinators, or both. Whether the species considered were characterized as social or solitary species or were a collection of species which included both social and solitary species.</i>  |
| <b><i>Sociality</i></b>       | <i>Whether the study explicitly measured/estimated the pollinator pollination contributions of ants (score=1) or not (score=0). The order of pollinator species. Possible levels/combinations include: Hymenoptera, Diptera, Coleoptera, Formicidae, Lepidoptera, Thysanoptera, Apodiformes, Odonata, and Hemiptera. (Each order is a binary (yes/no) variable). If the enumerated pollinator community included at least one species for a given order, score = 1, otherwise score = 0.</i>   |
| <b><i>Ants</i></b>            | <i>The plant name(s) of study target species target plant (crop) specie(s). If pollination services were estimated with respect to the species (e.g. coffee) in question, score = 1, otherwise score = 0. E.g. Acerola, Coffee, Pigeonpea, Coffee, Watermelon, Macadamia etc. (Each plant is a binary (yes/no) variable).</i>  |
| <b><i>Order</i></b>           | <i>Whether the target plant species (crop) is herbaceous (score=1) or woody (score=0)</i>  |
| <b><i>Plant</i></b>           | <i>Whether the target plant species (crop) bears fruit (score=1) or not (score=0)</i>  |
| <b><i>Herb</i></b>            | <i>Whether the target plant species (crop) bears nut(s) (score=1) or not (score=0)</i>   |
| <b><i>Fruit</i></b>           | <i>Whether the target plant species (crop) floral reward for pollinators was oil (score=1) or not (score=0)</i>  |
| <b><i>Nut</i></b>             | <i>Whether the target plant species (crop) floral reward for pollinators was nectar (score=1) or not (score=0)</i>   |
| <b><i>Oil</i></b>             | <i>Whether the target plant species (crop) floral reward for pollinators was pollen (score=1) or not (score=0)</i>   |
| <b><i>Nectar</i></b>          | <i>Whether the target plant species (crop) is commercial (e.g. sold in agriculture )) (score=1) or not (score=0)</i>   |
| <b><i>Pollen</i></b>          | <i>Whether the target plant species (crop) is able to self-pollinate (however pollination may however increase seed production) (score=1) or is self-incompatible (score=0)</i>  |
| <b><i>Commercial</i></b>      |  |
| <b><i>Self-Compatible</i></b> |  |

|  |   |
|--|---|
| <b>Outcrossing<br/>(cross pollination)</b> | <i>Whether the target plant species (crop) requires outcrossing (via pollinators or Wind-obligate outcrosser) (score=1) or may inbreed (score=0)</i>  |
| <b>Pesticide use</b>                       | <i>Whether the target plant species (crop) was sprayed with a pesticide (not as part of the study necessarily) or not.</i>  |
| <b>Fertilizer</b>                          | <i>Whether the target plant species (crop) in the study were given fertilizer or not fertilized.</i>  |
| <b>Buzz</b>                                | <i>Whether the buzz pollination was used. Possible levels include: used, not used, and unknown.<br/>(score=1) or not (score=0)</i>  |
| <b>Mating System</b>                       | <i>The type of mating system employed by plant species (crop)<br/>Possible levels include: Monoecious, Dioecious, Hermaphroditic, Polygamoecious, and Andromonoecious.</i>  |
| <b>Pollination measurement indicator</b>   | <i>The type of pollination endpoint indicator measured in the study.<br/>Possible levels include: fruit set, seed mass, seed set, seed/pollination deficit, number of flowers, fruit weight, pollen grains, pollen efficiency/deposition, and fertilization rate.</i>         |
| <b>Pollinator community attribute</b>      | <i>The type of indicator used to measure pollinators. The measured/estimated attribute of the pollinator community. Possible levels include: abundance (visits, individuals, biomass), richness, Shannon diversity, presence/absence (Exclusion), abundance and richness.</i> |

Table 3.4. Bivariate associations between estimated effect size (ES) and candidate moderators based on a sub-sample of 173 effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE), and test of moderators and associated type I error rate(QM,  $p$ ).

| <b>Model</b>                            | Log-Likelihood | AIC    | $R^2$<br>analog | QE*     | QM, $p$        |
|---|----------------|--------|-----------------|---------|----------------|
| ES~Null                                 | -203.063       | 410.13 |                 |         |                |
| ES~Mixed                                | -182.63        | 371.26 | 0.15            | 2570.47 | 44.76, <0.0001 |
| ES~Pollination measurement<br>indicator | -182.87        | 379.73 | 0.19            | 2411.05 | 46.12, <0.0001 |
| ES~Pollinator community attribute       | -186.97        | 385.94 | 0.2             | 2386.77 | 38.86, <0.0001 |
| ES~Culture type                         | -185.92        | 379.84 | 0.12            | 2629.57 | 37.19, <0.0001 |
| ES~Buzz                                 | -188.96        | 383.92 | 0.16            | 2565.48 | 32.54, <0.0001 |
| ES~Year                                 | -190.55        | 387.11 | 0.13            | 2617.43 | 28.19, <0.0001 |
| ES~Hives                                | -194.18        | 394.37 | 0.1             | 2689.92 | 20.07, <0.0001 |
| ES~Pesticide                            | -197.11        | 400.23 | 0.05            | 2871.91 | 12.72, 0.0004  |
| ES~Thysanoptera                         | -197.73        | 401.47 | 0.01            | 2992.32 | 10.81, 0.001   |
| ES~Herb                                 | -198.44        | 402.88 | 0.08            | 2770.63 | 10.77, 0.001   |
| ES~P_Native                             | -198.82        | 403.63 | 0.1             | 2696.11 | 10.67, 0.001   |
| ES~Commercial                           | -198.86        | 403.73 | 0.04            | 2895.74 | 9.03, 0.003    |
| ES~Fruit                                | -199.79        | 405.58 | 0.03            | 2895.36 | 7.07, 0.01     |
| ES~Odonata                              | -200.18        | 406.35 | 0.02            | 2955.65 | 6.06, 0.01     |
| ES~Lepidoptera                          | -200.23        | 406.47 | 0               | 3009.19 | 5.62, 0.02     |
| ES~Apodiformes                          | -200.87        | 407.74 | 0.08            | 2768.31 | 5.85, 0.02     |
| ES~Hemiptera                            | -200.87        | 407.74 | 0.08            | 2768.31 | 5.85, 0.02     |
| ES~Diptera                              | -201.14        | 408.29 | 0.04            | 2890.27 | 4.45, 0.04     |
| ES~Pvisit                               | -201.59        | 409.18 | 0.02            | 2944.47 | 3.17, 0.08     |
| ES~Ants                                 | -201.78        | 409.56 | 0.01            | 2983.95 | 2.65, 0.1      |
| ES~Coleoptera                           | -201.87        | 409.73 | 0.03            | 2908.49 | 2.85, 0.09     |

\* For all QE,  $p < 0.0001$

Table 3.5. Bivariate associations between estimated effect size (ES) and multiple candidate models involving linear combinations of the top eight moderators. Shown are model log likelihood, Second order Akaike Information Criterion (AICc),  $R^2$  analog, Delta AIC, Akaike weights and evidence ratios.

| <b>Model</b>  | Log-Likelihood | AICc   | $R^2$ analog | $\Delta$ AIC | $W_i$ | Evidence Ratio |
|---|----------------|--------|--------------|--------------|-------|----------------|
| ES~Pollination measurement indicator+Pollinator community attribute+Buzz+Year         | -154.57        | 337.08 | 0.38         | 0.00         | 0.39  |                |
| ES~Pollination measurement indicator+Buzz+Year  | -160.48        | 339.84 | 0.36         | 2.76         | 0.10  | 3.93           |
| ES~Pollination measurement indicator+Pollinator community attribute+Culture type+Year | -154.87        | 340.02 | 0.39         | 2.94         | 0.09  | 4.32           |
| ES~Pollination measurement indicator+Buzz+Year +Hives                                 | -159.65        | 340.41 | 0.35         | 3.33         | 0.07  | 5.25           |
| ES~Pollination measurement indicator+Pollinator community attribute+Mixed+Year        | -156.27        | 340.49 | 0.36         | 3.41         | 0.07  | 5.46           |
| ES~Pollination measurement indicator+Buzz+Year +Mixed                                 | -160.01        | 341.12 | 0.36         | 4.04         | 0.05  | 7.46           |
| ES~Pollination measurement indicator+Mixed+Hives+Year                                 | -160.47        | 342.05 | 0.34         | 4.97         | 0.03  | 11.90          |
| ES~Pollination measurement  | -161.60        | 342.08 | 0.34         | 5.00         | 0.03  | 12.10          |

indicator+Mixed+Year

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -158.33 | 342.30 | 0.34 | 5.22 | 0.03 | 13.48 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Pollinator community  
attribute+Mixed

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -156.11 | 342.50 | 0.37 | 5.42 | 0.03 | 14.92 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Pollinator community  
attribute+Culture type+Mixed

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -161.86 | 342.60 | 0.34 | 5.52 | 0.02 | 15.65 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Hives+Year

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -159.75 | 342.85 | 0.35 | 5.77 | 0.02 | 17.76 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Culture  
type+Hives+Year

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -159.75 | 342.86 | 0.37 | 5.78 | 0.02 | 17.80 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Culture type+Buzz+Year

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -157.74 | 343.44 | 0.36 | 6.36 | 0.02 | 23.79 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Pollinator community  
attribute+Hives+Year

|                            |         |        |      |      |      |       |
|----------------------------|---------|--------|------|------|------|-------|
| ES~Pollination measurement | -157.91 | 343.77 | 0.34 | 6.69 | 0.01 | 28.15 |
|----------------------------|---------|--------|------|------|------|-------|

indicator+Pollinator community  
attribute+Mixed+Buzz

Table 3.6. Bivariate associations between estimated effect size (ES) and candidate moderators based on the sub-sample of 112 effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE), and test of moderators and associated type I error rate(QM,  $p$ ).

| <b>Model</b>                         | Log-Likelihood | AIC    | $R^2$ analog | QE*     | QM, $p$        |
|--------------------------------------|----------------|--------|--------------|---------|----------------|
| ES~NULL                              | -126.22        | 256.43 |              |         |                |
| ES~Pollination measurement indicator | -112.35        | 238.7  | 0.19         | 937.02  | 32.78, <0.0001 |
| ES~Buzz                              | -118.44        | 242.87 | 0.14         | 1035.47 | 18.67, <0.0001 |
| ES~Pesticide use                     | -118.48        | 242.98 | 0.16         | 1011.5  | 19.22, <0.0001 |
| ES~Mixed                             | -121.5         | 249    | 0.08         | 1105.96 | 10.79, 0.00    |
| ES~N_ind/vis                         | -122.45        | 250.91 | 0.05         | 1129.02 | 8.43, 0.00     |
| ES~Sociality                         | -121.73        | 251.45 | 0            | 1170.21 | 8.95, 0.01     |
| ES~Pollinator community attribute    | -121.84        | 253.65 | 0.1          | 1056.33 | 10.71, 0.01    |
| ES~Lepidoptera                       | -124.58        | 255.16 | 0            | 1188.13 | 3.16, 0.08     |
| ES~Commercial                        | -124.77        | 255.55 | 0.02         | 1165.36 | 3.12, 0.08     |
| ES~Fruit                             | -124.9         | 255.79 | 0.02         | 1159.65 | 2.96, 0.09     |
| ES~St_Design                         | -124.995       | 255.99 | 0.06         | 1112.16 | 3.53, 0.06     |
| ES~Hives                             | -125.05        | 256.1  | 0.03         | 1158.94 | 2.75, 0.1      |
| ES~Culture type                      | -124.05        | 256.11 | 0.02         | 1158.6  | 4.57, 0.1      |

\* All  $p < 0.0001$

Table 3.7. Effect size and the associated within-study intraclass correlation (ICC) used to estimate within-study variance. Blank fields indicate studies for which only one effect size was calculated.

| Study | Study Name       | Effect   | Correlation | Variance |
|-------|------------------|----------|-------------|----------|
|       |                  | Size     | ICC         | $V_z$    |
|       |                  | z        |             |          |
| 1     | Vilhena          | 0.0445   |             | 0.0476   |
| 2     | Badano           | 0.2986   | 0.471494    | 0.0093   |
| 3     | Otieno           | 2.7825   |             | 0.0303   |
| 4     | Carvalho         | 0.5171   | 0.8861      | 0.0096   |
| 5     | Diekotter        | 0.2448   |             | 0.1111   |
| 6     | Vergara          | 1.9037   | 0.8855      | 0.0592   |
| 7     | Winfrey          | 0.7081   | 0.8561      | 0.0928   |
| 8     | Albrecht         | 0.3388   | 0.4270      | 0.0004   |
| 9     | Morandin2006     | 0.881374 |             | 0.052632 |
| 10    | Morandin2005     | 0.9113   | 0.9363      | 0.0389   |
| 11    | Mand             | 0.2053   | 0.9515      | 0.0296   |
| 12    | Philpott         | 0.0592   | 0.6539      | 0.0025   |
| 13    | Klein2003a       | 0.6083   | 0.8620      | 0.0120   |
| 14    | Klein2003b       | 0.5874   | 0.6972      | 0.0144   |
| 15    | Morandin2001     | 0.4545   | 0.9049      | 0.0595   |
| 16    | Klein2009        | 0.8852   | 0.8928      | 0.0169   |
| 17    | Veddeler         | 0.481212 |             | 0.055556 |
| 18    | Greenleaf        | 2.235352 | 0.372942    | 0.6865   |
| 19    | Larsen           | 0.907794 | 0.756588    | 0.0459   |
| 20    | Willmer          | 0.738803 | 0.907018    | 0.0144   |
| 21    | Steffan-Dewenter | 0.70853  | 0.692721    | 0.0044   |
| 22    | Javorek          | 2.66641  | 0.857018    | 0.0079   |
| 23    | Singh            | 3.183567 | 0.624808    | 0.0288   |
| 24    | Freitas          | 3.124717 |             | 0.00361  |
| 25    | Corbet           | 1.194763 |             | 0.017544 |
| 26    | Tepedino         | 0.271244 | 0.19084     | 0.1412   |
| 27    | Kakutani         | 0.562258 | 0.980841    | 0.0114   |
| 28    | Cavalcant        | 0.782    |             | 0.623209 |
| 29    | Heard1993        | 0.240546 | 0.85669     | 0.0125   |

|    |           |          |          |          |
|----|-----------|----------|----------|----------|
| 30 | Vithanage | 1.421926 |          | 0.2      |
| 31 | Free1976  | 1.027743 | 0.974784 | 0.0019   |
| 32 | Ewies     | 1.984244 | 0.597889 | 0.0515   |
| 33 | Raw       | 1.67956  | 0.945199 | 0.0019   |
| 34 | Free1975  | 0.231798 |          | 0.010753 |
| 35 | Heard1975 | 0.333786 | 0.984056 | 0.0022   |
| 36 | Nadel     | 0.947345 | 0.89849  | 0.0618   |
| 37 | Bhata     | 1.70821  | 0.675496 | 0.0366   |
| 38 | Hammer    | 0.4939   |          | 0.0053   |
| 39 | George    | 1.4722   |          | 0.0625   |

Table 3.8. Bivariate associations between estimated effect size (ES) and candidate moderators based on the sample of 39 synthetic effect sizes. Shown are model log-likelihood, associated Akaike Information Criterion (AIC),  $R^2$  analog, test for residual heterogeneity (QE), and test of moderators and associated type I error rate(QM,  $p$ ).

| Model           | Log-Likelihood | AIC    | $R^2$ analog | QE*     | QM, $p$        |
|-----------------|----------------|--------|--------------|---------|----------------|
| ES~NULL         | -49.19         | 102.39 |              |         |                |
| ES~Culture type | -40.03         | 90.06  | 0.45         | 1391.75 | 24.73, <0.0001 |
| ES~Pesticide    | -44.91         | 97.82  | 0.04         | 3524.34 | 8.53, 0.01     |
| ES~Mixed        | -47.99         | 101.99 | 0.17         | 2606.3  | 2.73, 0.1      |
| ES~Exclusion    | -47.46         | 100.92 | 0            | 3655.26 | 3.57, 0.06     |

\* All  $p < 0.0001$

## Figures

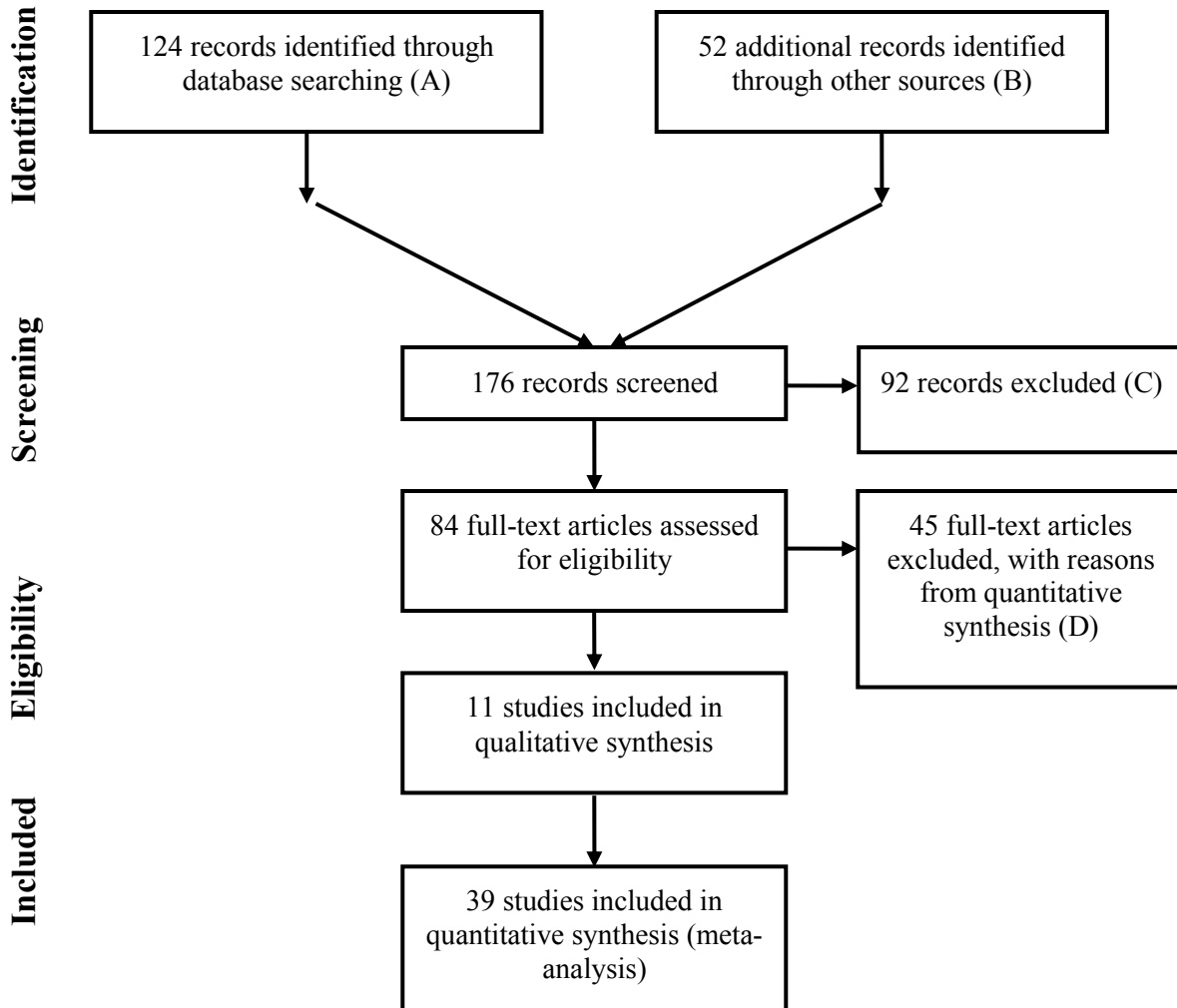


Figure 3.1. Flow chart indicating study identification based on study retrieval and screening and eligibility according to stated inclusion criteria and those studies included in a quantitative meta-analysis and qualitative analysis.

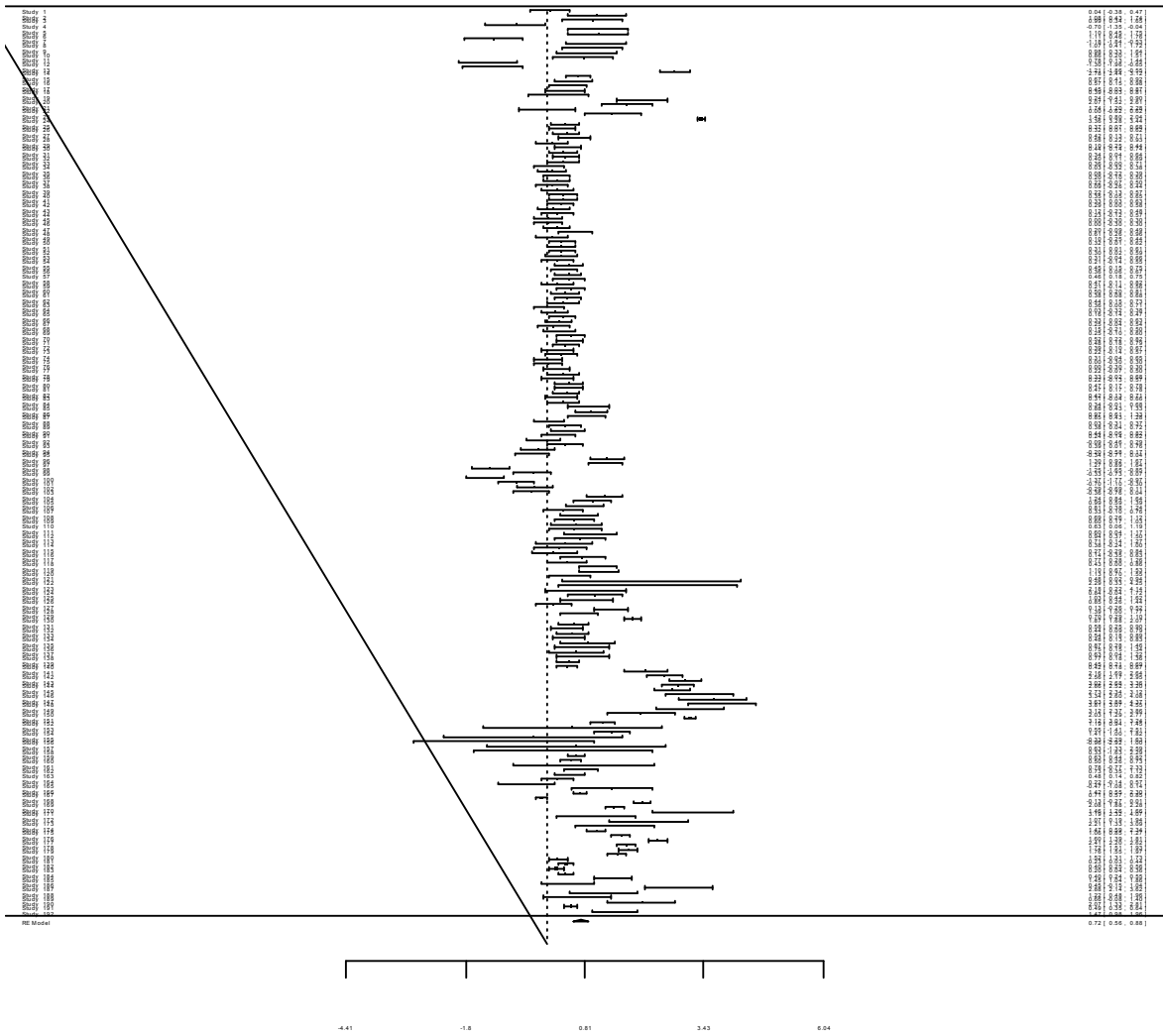


Figure 3.2. Forest plot showing Fisher's  $r$  to  $z$  transformed correlation coefficient effect sizes and summary effect (and associated confidence intervals) based on a fitted random effects model.

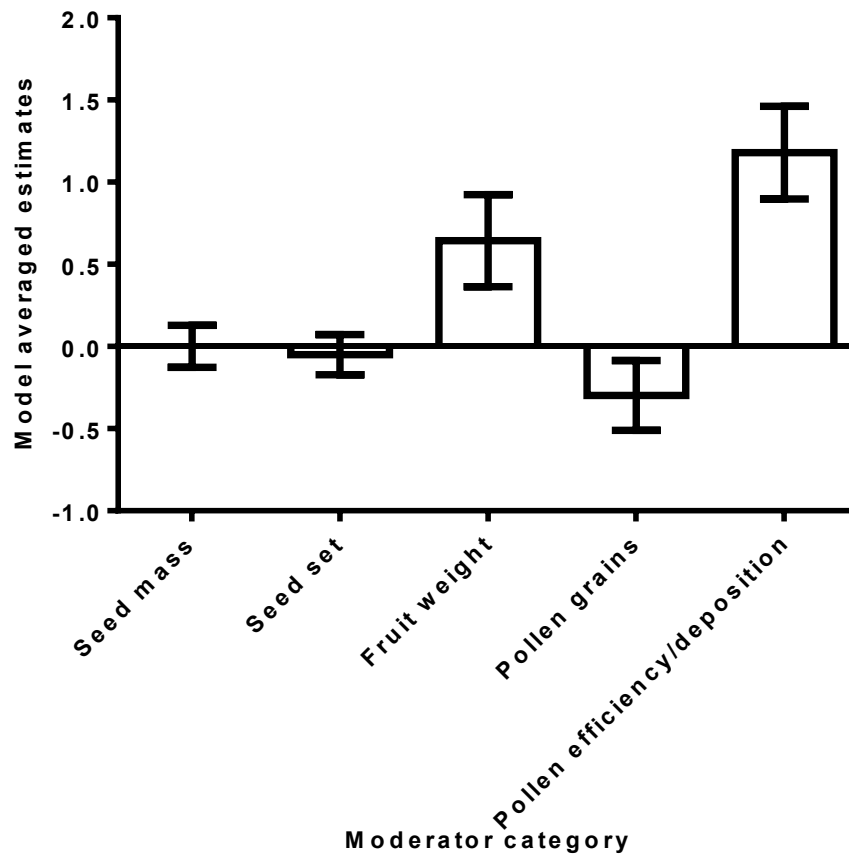


Figure 3.3. Model averaged coefficients (based on 101 models having some support) and associated standard errors) for each category of the pollination measurement indicator moderator (reference category is fruit set).

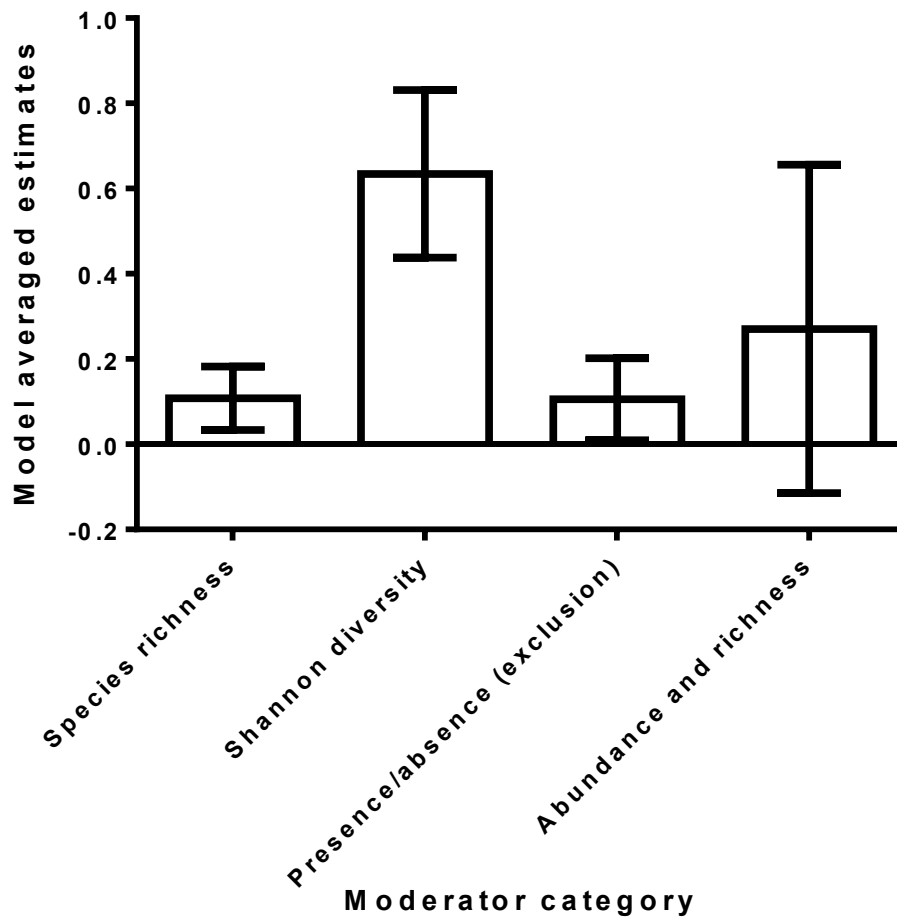


Figure 3.4. Model averaged coefficients (based on 101 models having some support) and associated standard errors) for each category of the pollinator measurement attribute moderator (reference category is abundance).

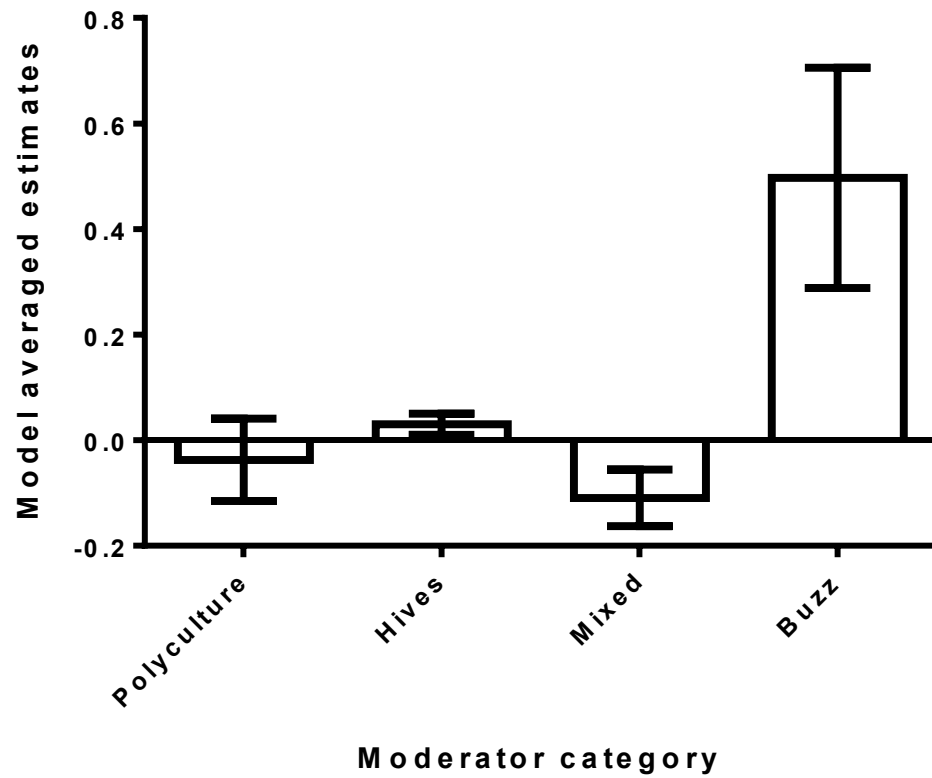


Figure 3.5. Model averaged coefficients (based on 101 models having some support) and associated standard errors) for type of culture (reference category is monoculture), presence of managed pollinator populations (hives), mixed culture with natural vegetation (reference category in no natural intercropped natural vegetation), and the presence of buzz pollination.

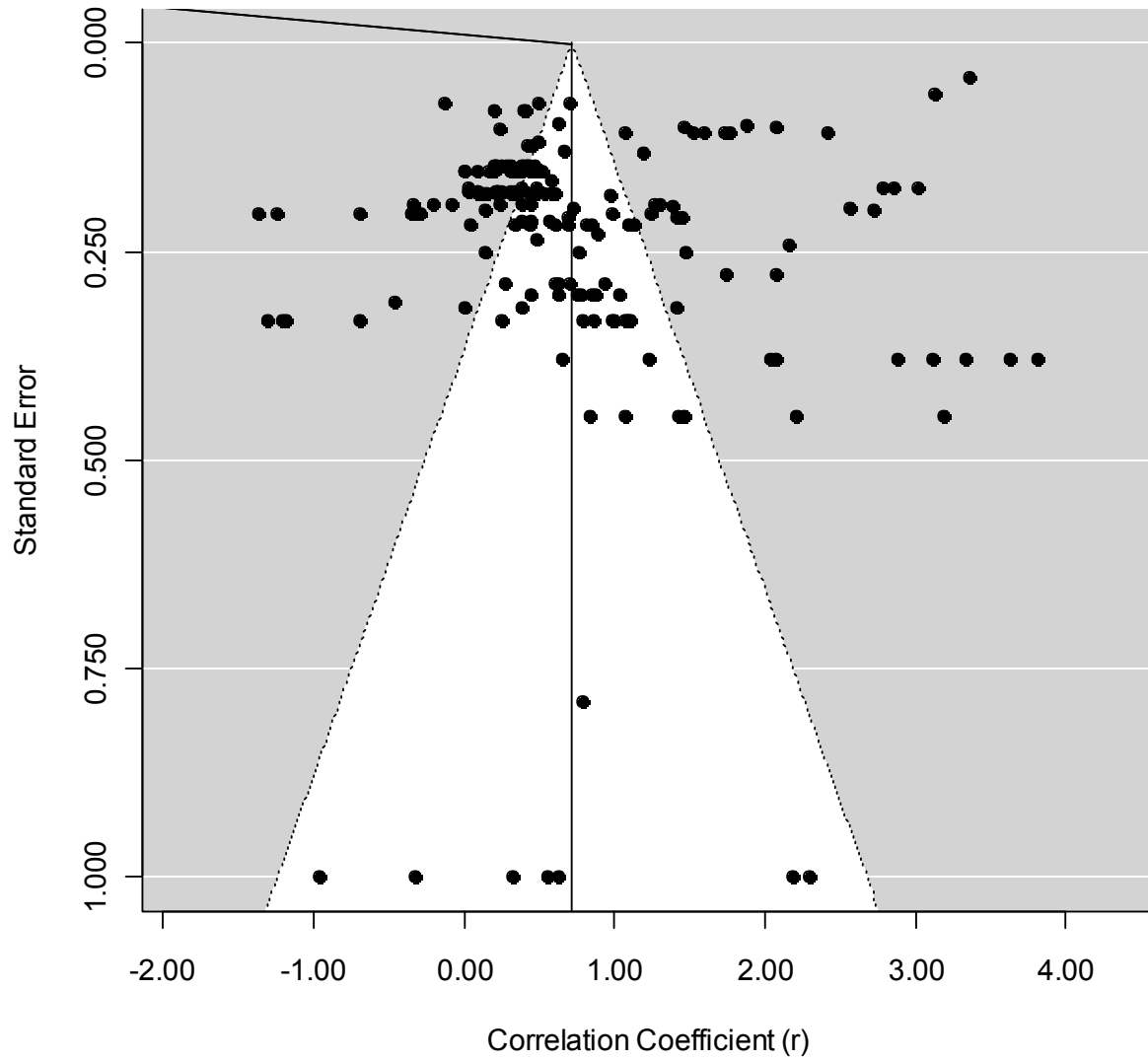


Figure 3.6. Funnel plot of the estimated standard error of the effect size versus the Fisher z-transformed effect size estimate.

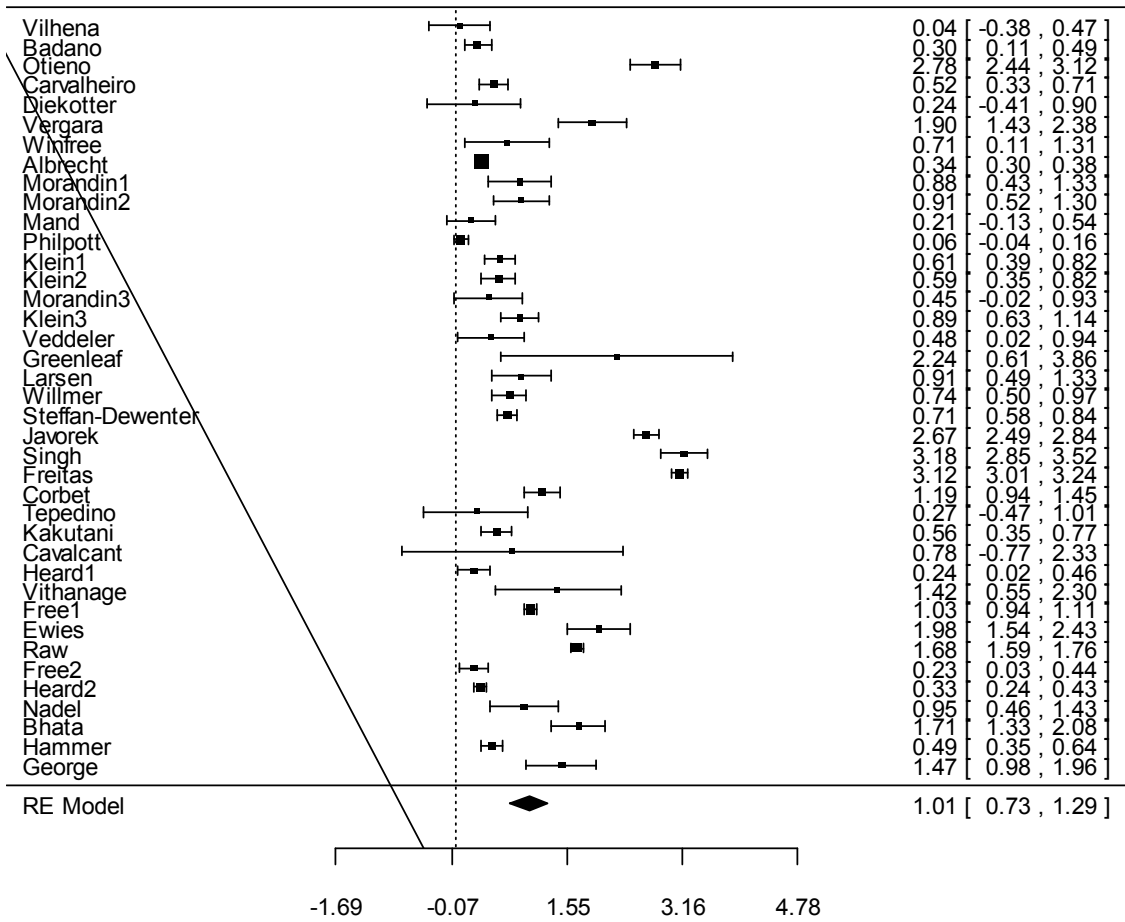


Figure 3.7. Forest plot showing  $r$  to Fisher's  $z$  transformed correlation coefficient based on estimated synthetic effect sizes (and associated confidence intervals) at the study level under a random effects model.

## Summary and conclusion

In this thesis, I have attempted to provide a starting place for estimate levels of specific ecosystems services, as well as develop models to predict service levels based on measurable attributes of either: the system itself, the study design, or the endpoints from which the level of service is inferred. I employed a meta-analytical approach to examine two specific ecosystem service/ecosystem type case studies: flood control provisioning by wetlands and pollination service provisioning by natural pollinator populations in agroecosystems. In addition, I set out to determine the relationship in research effort between environmental science and ecological economics.

In my first chapter, based on the assumption that valuation of ecosystem services requires, first and foremost, that the current level or stock of a service first be estimated, I provide a quantitative assessment of the relationship between the effort expended by environmental scientists and ecological economists on different ecosystem types and services using hits in bibliographic databases as a coarse measure of research effort. I found a positive, moderately strong correlation between research efforts in the two domains, a result that, while encouraging, is more likely to reflect serendipity than the deliberate design of integrated environmental science-environmental economics research programs on ecosystem services.

Although my results indicate that, at least at a coarse level, environmental scientists and ecological economists may at least be pulling in the same direction, I believe that greater efficiency may yet still be achieved by means of a global ecosystem service research network and repository. Such a repository would explicitly link research in the biophysical sciences on the measurement and prediction of ecosystem functions with that of the social sciences on the valuation of ecological services via three separate link attributes: (a) geospatial and temporal location; (b) ecosystem type(s) and; (c) ecosystem services and associated ecosystem functions. Such a repository would allow researchers in the biophysical sciences to link directly with researchers interested in the development and application of methods to estimate the economic value of such services. Moreover, such a network would, at least in principle, facilitate a more efficient research agenda wherein

economists focus on ecosystems and their associated services for which the current scientific understanding permits some level of prediction about, minimally, current service levels; and environmental scientists focus on ecosystems and their associated services for which validated economic valuation tools exist and can be expeditiously deployed.

In chapter 2, I evaluate the level of flood control services provided by wetlands using a meta-analysis of the primary literature. I found that, on average, consistent with conventional wisdom, wetlands do indeed have a positive effect by reducing the frequency and magnitude of floods, increasing low flows, and increasing water storage. My results also indicate that, at current levels of understanding, the predictive power of meta-analytic models to predict the level of service provided by a specific wetland is modest at best. This, combined with the heterogeneity in effect sizes means that predictions concerning the flood control service provided by a wetland and the expected change in the level of service under a candidate management scenario, will have comparatively large uncertainty.

In chapter 3, I estimate the level of pollination services delivered by natural pollinator populations in agro-ecosystems. On the basis of a comprehensive meta-analysis of the published literature, I find that, on average and consistent with conventional wisdom, that there is a consistent and comparatively strong association between pollinator diversity and agroecosystem productivity as inferred from measures of plant pollination success. Metaregression analysis indicates, however, that our current ability to estimate the level of pollination services provided by native pollinator populations is comparatively poor. This, combined with the large inter-study heterogeneity in effect sizes means that predictions about the current level of pollination services delivered by natural pollinator populations in particular agro-ecosystems, as well as predictions about how the level of such services will change with reduced (or enhanced) natural pollinator population abundance, will have large uncertainty. Such uncertainty should be explicitly incorporated into estimates of both the current economic value of pollination services delivered by natural pollinator populations in agro-ecosystems, as well as estimates of how this value is likely to change under alternative management scenarios.

The ecosystem service approach, as originally proposed (Costanza and Daly 1992, Perrings et al. 1992, Costanza et al. 1997), offers some promise of preserving the planet's diminishing natural capital. Making good on this promise requires evidence that natural ecosystems (a) do indeed provide substantial levels of ecological services; (b) that the economic value of the services so provided by ecosystems in a more or less natural state is greater than the economic value of the same ecosystem in a transformed state. Only when these two conditions are met will decision-makers concerned principally with economic welfare be motivated to maintain, and possibly enhance, the natural capital of the world's ecosystems. My research has provided, for two different ecosystems and two different services, evidence for (a). On the other hand, it also suggests that predicting the change in the level of services provided under alternate ecosystem management regimes may be difficult indeed, with any such predictions carrying comparatively large uncertainty. In short, while my results provide substantial evidence of the provisioning of flood control services by wetlands and of pollination services by natural native pollinator populations, the precise level of these services provided by a particular wetland, or by a specific pollinator community for a specific agroecosystem, is much more difficult to predict. Even more difficult will be accurate (and precise) predictions about how the levels of services will change with, for example, changes in the biophysical attributes of wetlands or the structure and composition of native pollinator communities.

This lack of predictability itself has important implications. Ecological economics is concerned largely with providing quantitative estimates of the economic value of ecosystem services per unit service provided (or some proxy thereof, for example, the annual per hectare value of wetlands (e.g. Olewiler 2004, Molnar et al. 2012)). A quantitative estimate of total value is then obtained by multiplying the unit economic value by the estimated amount of service provided by the system in its current states and, ideally, under alternate states. Yet my results suggest that, in the absence of highly detailed, ecosystem- and service-specific biophysical information, any quantitative estimate of the level of service provided – especially under alternate states/management regimes -may be so imprecise that the estimate itself is of comparatively little quantitative value. This in turn

implies that to the extent that decision-making is informed by such estimates, it would be sensible to adopt a coarse-grained, qualitative approach to the characterization of the outcome space (unit) used by economists, and to avoid any attempts to define the quantitatively “optimal” solution much favoured by economists, and not a few ecologists. My suspicion is that the precision required to justify any such approach will invariably be lacking; as such, both economists and ecologists are well-advised to look to other approaches in informing decisions on ecosystem management.

## References

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## Appendix A. Ecosystem Classification System

I employed an ecosystem classification system very similar to that of the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005a): Forest (Boreal, Temperate, Tropical), Dryland (Temperate grassland, Mediterranean, Tropical Grassland and Savanna, Desert), Inland Water, Coastal, Marine, Island, Mountain, Polar. The inland water class was replaced with more refined ecosystem types (lakes, bays and ponds). More refined ecosystem sub-types were defined based on the World Wildlife Fund classification scheme (Abell et al. 2008, Spalding et al. 2007, Olson et al. 2001) to create 11 broad ecosystem classes and 49 subclasses.

### **Broad Ecosystem**

#### **Class (coarse)**

#### **(Fine) Ecosystem Subclasses**

Coastal

Coral Reefs  
Estuaries  
Intertidal-Littoral  
Kelp  
Lagoons and Salt Ponds  
Mangrove  
Rock and Shell Reefs  
Seagrass

Dryland/Terrestrial (terrestrial added as a synonym)

Desert  
Grassland, Steppe, Prairie (steppe and prairie terms added to Millennium Ecosystem Assessment classification)  
Mediterranean  
Savanna  
Shrubland/Chaparral  
Temperate Grassland, Savanna, Shrubland  
Tropical/Subtropical Grassland, Savanna, Shrubland  
Tundra

Forest/Woodlands (woodlands added as a synonym)

Boreal/Taiga  
Broadleaf  
Coniferous  
Mixed  
Temperate  
Tropical/Subtropical

|         |  |
|---------|--|
| Island  |  |
| Lake    | Bay  |
|         | Pond                                       |
| Polar   |  |
| River   |  |
|         | Coastal                                    |
|         | Delta                                      |
|         | Lowland                                    |
|         | Stream                                     |
|         | Temperate                                  |
|         | Tropical/Subtropical                       |
|         | Upland                                     |
| Wetland | (tried to capture all wetland types)       |
|         | Bog  |
|         | Fen  |
|         | Ephemeral                                  |
|         | Flooded Grasslands and Savannas/Floodplain |
|         | Marsh                                      |
|         | Peatland                                   |
|         | Riparian Zone                              |
|         | Swamp                                      |
|         | Vernal                                     |

And by some of my own additions to ensure a comprehensive range of ecosystem types:

|            |                   |
|------------|-------------------|
| Cultivated |                   |
|            | Agricultural      |
|            | Agroecosystem     |
|            | Cropland          |
|            | Pasture/Rangeland |
| Marine     |                   |
|            | Ocean             |
|            | Sea               |
| Mountain   |                   |
|            | Alpine            |
|            | Highland          |
|            | Montane           |

**Appendix B. Description of each candidate predictor variable and associated metadata.**

Each quantitative effect size was given an entry into a database which was constructed to emulate the review constructed by Bullock and Acreman (2003). Additional fields (and predictor variables) were created aside from those taken I adopted from classification system developed Bullock and Acreman (2003) for wetland type, wetland study and basis of inference. Every effect size that could be calculated was given entry into the database even if it was missing data for certain variables.

Table 1 provides a list of candidate predictor variables used in this study. For descriptions of categories: Wetland Type, Wetland Study, Local Term, and Basis of Inference please see reference Bullock and Acreman (2003) (several categories removed and/or condensed).

|                           |   |   |                                |   |                              |   |            |   |
|---------------------------|---|---|--------------------------------|---|------------------------------|---|------------|---|
| <b>Wetland Type</b>       | Surface Water and Groundwater slope and depressions | 0 | Surface Water Depression/Slope | 1 | Groundwater Depression/Slope | 2 | Floodplain | 4 |
| <b>Wetland Study</b>      | Conceptual catchment model                          | 0 | Long-term hydrograph           | 1 | Component process            | 2 |            |   |
| <b>Basis of Inference</b> | With/out  | 0 | Drained                        | 1 | Pair/Multiple                | 2 | Dam-No Dam | 3 |

|                   |             |   |       |   |       |   |        |   |     |   |      |   |     |   |      |   |         |   |
|-------------------|-------------|---|-------|---|-------|---|--------|---|-----|---|------|---|-----|---|------|---|---------|---|
| <b>Local Term</b> | Paddy Field | 0 | Dambo | 1 | Marsh | 2 | Pakihi | 3 | Bog | 4 | Peat | 5 | Fen | 6 | Wadi | 7 | Wetland | 8 |
|-------------------|-------------|---|-------|---|-------|---|--------|---|-----|---|------|---|-----|---|------|---|---------|---|

Study Type: An ‘Empirical’ study is one in which wetland(s) were observed or experimented with in the field. A ‘Modelled’ study refers to one in which wetland(s) were observed of experimented on using computational simulations. In these general modelled studies parameters were not based on a specific natural wetland. A ‘Modelled from

Empirical' study is one in which hydrological processes are simulated/modelled based on existing empirical parameters of a natural wetland.

|           |   |          |   |                         |   |
|-----------|---|----------|---|-------------------------|---|
| Empirical | 0 | Modelled | 1 | Modelled from Empirical | 2 |
|-----------|---|----------|---|-------------------------|---|

Study Design: A category labelled 'Before-After' is a study which takes the simplest approach of collecting data prior to an activity and compares it with the data after the activity. A category 'Control-Impact' is the comparison of data in one system which has not been manipulated with another system where an impact or impacts have been added to the system. A category 'Before-After/Control-Impact' uses both of these designs and compares data before and after an impact or impacts have been added to the system.

|    |   |    |   |      |   |
|----|---|----|---|------|---|
| BA | 0 | CI | 1 | BACI | 2 |
|----|---|----|---|------|---|

Flood Event: is considered 'Extreme' when it occurs during a Natural Disaster-Cyclone, Hurricane, and Typhoon etc. is specifically stated in study. All other occurrences which do not specifically indicate large storm systems are denoted 'Natural'.

|         |   |         |   |
|---------|---|---------|---|
| Natural | 0 | Extreme | 1 |
|---------|---|---------|---|

Study Control: Studies categorized as 'Parameters not fixed' did not manipulate any variables that went into the inference of the study-natural system or experimentation. Studies deemed 'Parameters fixed' had controlled one of the drivers of the system (e.g. the rate of discharge entering a wetland was fixed at a certain number)

|                      |   |                  |   |
|----------------------|---|------------------|---|
| Parameters not fixed | 0 | Parameters fixed | 1 |
|----------------------|---|------------------|---|

Hydrological measures: were categorized into those studies dealing with 'Discharge'-volume rate of water flow, 'Peak Flow'-the peak flow of discharge during a hydro-period, 'Low Flow'-the minimum point of water flow over a hydro-period, 'Runoff'-the flow that occurs when the soil has reached its infiltration capacity, 'Time to Peak'-time from return of flood OR time from onset to peak of flood.

|           |   |           |   |          |   |        |   |              |   |
|-----------|---|-----------|---|----------|---|--------|---|--------------|---|
| Discharge | 0 | Peak Flow | 1 | Low Flow | 2 | Runoff | 3 | Time to Peak | 4 |
|-----------|---|-----------|---|----------|---|--------|---|--------------|---|

PSHB Threshold: ‘No threshold effect’ indicates that the effect size is not limited by the size of the wetland and/or the volume or magnitude of the flood event. ‘Threshold effect’ is categorized for an effect size that IS limited by the size of the wetland and/or the volume or magnitude of the flood event (e.g. during a hurricane the size of a wetland can be irrelevant and vice versa).

|                     |   |                  |   |
|---------------------|---|------------------|---|
| No threshold effect | 0 | Threshold effect | 1 |
|---------------------|---|------------------|---|

Wetland Order: A ‘Headwater Wetland’ is categorized as any wetland that is not a floodplain. A ‘floodplain’ is a flat or nearly flat surface of land neighbouring a stream or river and usually does not store water year round unless it experiences high periods of flooding or discharge.

|                   |   |            |   |
|-------------------|---|------------|---|
| Headwater Wetland | 0 | Floodplain | 1 |
|-------------------|---|------------|---|

Country: Categorized by the country the study took place in

Sample size: the number of measurements included in the analysis

Wetland area: the total size of wetlands (ha) used in the analysis

Study Size: the total size of the area (ha) investigated in the study

Year: year in which the study was published

**Set of Predictor variables and associated unit or variable type and associated categories (levels).**

| Predictor Variables | Units          | Categories   |
|---------------------|----------------|--|
| Study Type          | Categorical... | <i>Empirical, Modelled, Modelled from Empirical Data</i>   |
| Wetland Type        | ...            | <i>Surface Water Depression/Slope And Groundwater Depression/Slope, Surface Water Depression/Slope, Groundwater Depression/Groundwater Slope, Floodplain</i> |

|                       |          |   |
|-----------------------|----------|---|
| Study Design          | ...      | <i>Before-After, Control-Impact, Before-After/Control-Impact</i>  |
| Wetland Study         | ...      | <i>Conceptual catchment model, Water balance, Long-term hydrograph, Single event hydrograph, Trend analysis in time series, Component process</i> |
| Local Term            | ...      | <i>Paddy Field, Dambo, Marsh, Pakihi, Bog, Peat, Fen, Wadi, Wetland</i>   |
| Flood Event           | ...      | <i>Natural, Extreme</i>   |
| Study Control         | ...      | <i>Parameters not fixed, Parameters fixed</i>   |
| Basis of Inference    | ...      | <i>With/out, Drained, Pair, Multiple, In-out, Same, Dam-No Dam, Comp<sup>a</sup></i>  |
| Hydrological Endpoint | ...      | <i>Discharge, Peak Flow, Low Flow, Runoff, Time to Peak</i>   |
| PSHB threshold        | ...      | <i>No threshold effect, Threshold effect</i>  |
| Wetland Order         | ...      | <i>Headwater Wetland, Floodplain</i>  |
| Country               | ...      | <i>China, Belgium, Malawi, United States, New Zealand etc.</i>  |
| Sample Size           | ...      | <i>Continuous...</i>  |
| Wetland Area          | hectares | ...   |
| Study Size            | hectares | ...   |
| Year of Study         | Year     | ...   |

**Appendix C. Model results of the predictor moderators showing bivariate influence on effect size when all effect sizes are analyzed (k=40).**

| <b>Model</b>   | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b> | <b>ci.lb</b> | <b>ci.ub</b> |    |
|--|-----------------|-----------|----------|----------|--------------|--------------|----|
| <b>ES~Wetland type</b>   |                 |           |          |          |              |              |    |
| intrcpt(SWDS+GWDS)   | 0.27            | 0.23      | 1.20     | 0.23     | -0.17        | 0.72         |    |
| factor(Surface Water Depression/Slope)                               | -0.10           | 0.31      | -0.31    | 0.75     | -0.70        | 0.51         |    |
| factor(Groundwater Depression/Slope)                                 | 0.53            | 0.32      | 1.67     | 0.09     | -0.09        | 1.14         |    |
| factor(Floodplain)   | -0.31           | 0.37      | -0.85    | 0.39     | -1.04        | 0.41         |    |
| <b>ES~Study control</b>  |                 |           |          |          |              |              |    |
| intrcpt (Parameters not fixed)                                       | 0.21            | 0.14      | 1.45     | 0.15     | -0.07        | 0.49         |    |
| factor(Parameters fixed)   | 0.44            | 0.26      | 1.70     | 0.09     | -0.07        | 0.94         |    |
| <b>ES~Study type</b>   |                 |           |          |          |              |              |    |
| intrcpt (Empirical)  | 0.19            | 0.14      | 1.34     | 0.18     | -0.09        | 0.47         |    |
| factor (Modelled)  | 0.55            | 0.29      | 1.89     | 0.06     | -0.02        | 1.11         |    |
| factor(Modelled from Empirical)                                      | 0.34            | 0.42      | 0.76     | 0.44     | -0.51        | 1.16         |    |
| <b>ES~Publication year</b>   |                 |           |          |          |              |              |    |
| Intrcpt  | -30.19          | 22.10     | -1.37    | 0.17     | -73.50       | 13.11        |    |
| data(Year)   | 0.02            | 0.01      | 1.38     | 0.17     | -0.01        | 0.04         |    |
| <b>ES~Wetland order</b>  |                 |           |          |          |              |              |    |
| intrcpt (Headwater Wetland)  | 0.42            | 0.13      | 3.18     | 0.00     | 0.16         | 0.67         | ** |
| factor(Floodplain)   | -0.45           | 0.33      | -1.38    | 0.17     | -1.10        | 0.19         |    |
| <b>Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</b> |                 |           |          |          |              |              |    |

**Appendix D. Model results of the predictor moderators showing bivariate influence on effect size when a sub-sample of effect sizes are analyzed (k=25).**

| <b>Model</b>   | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b> | <b>ci.lb</b> | <b>ci.ub</b> |     |
|--|-----------------|-----------|----------|----------|--------------|--------------|-----|
| <b>ES~Study type</b>   |                 |           |          |          |              |              |     |
| intrcpt (Empirical)  | 0.19            | 0.15      | 1.22     | 0.22     | -0.11        | 0.48         |     |
| factor (Modelled)  | 1.85            | 0.43      | 4.29     | <.0001   | 1            | 2.69         | *** |
| factor(Modelled from Empirical)                                      | 0.36            | 0.39      | 0.91     | 0.362    | -0.41        | 1.13         |     |
| <b>ES~Study control</b>  |                 |           |          |          |              |              |     |
| intrcpt (Parameters not fixed)                                       | 0.17            | 0.18      | 0.99     | 0.32     | -0.17        | 0.52         |     |
| factor(Parameters fixed)   | 1.1             | 0.35      | 3.14     | 0.002    | 0.41         | 1.79         | **  |
| <b>ES~Basis of inference</b>   |                 |           |          |          |              |              |     |
| intrcpt(With/out)  | 1.56            | 0.41      | 3.79     | 0.0001   | 0.76         | 2.37         | *** |
| factor(Drained)  | -1.46           | 0.61      | -2.38    | 0.02     | -2.66        | -0.26        | *   |
| factor(Pair/Multiple)  | -1.28           | 0.46      | -2.79    | 0.01     | -2.18        | 0.38         | **  |
| factor(Dam-No Dam)   | -1.28           | 0.69      | -1.85    | 0.07     | -2.64        | 0.08         | .   |
| <b>ES~Wetland type</b>   |                 |           |          |          |              |              |     |
| intrcpt(SWDS+GWDS)   | 0.27            | 0.26      | 1.03     | 0.30     | -0.24        | 0.79         |     |
| factor(Surface Water Depression/Slope)                               | -0.01           | 0.40      | -0.02    | 0.99     | -0.79        | 0.77         |     |
| factor(Groundwater Depression/Slope)                                 | 1.09            | 0.47      | 2.35     | 0.02     | 0.18         | 2.01         | *   |
| factor(Floodplain)   | -0.22           | 0.62      | -0.36    | 0.72     | -1.43        | 0.99         |     |
| <b>ES~Publication year</b>   |                 |           |          |          |              |              |     |
| intrcpt  | -81.89          | 46.73     | -1.75    | 0.08     | -174.48      | 9.71         | .   |
| data(Year)   | 0.04            | 0.02      | 1.76     | 0.08     | -0.01        | 0.09         | .   |
| <b>Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</b> |                 |           |          |          |              |              |     |

**Appendix E. Model results of the predictor moderators showing bivariate influence on effect size when synthetic effect sizes are analyzed (k=20).**

| <b>Model</b>  | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b> | <b>ci.lb</b> | <b>ci.ub</b> |
|---|-----------------|-----------|----------|----------|--------------|--------------|
| <b>ES~Study control</b>                                       |                 |           |          |          |              |              |
| intrcpt (Parameters not fixed)                                | 0.28            | 0.24      | 1.15     | 0.25     | -0.2         | 0.75         |
| factor(Parameters fixed)                                      | 0.43            | 0.39      | 1.1      | 0.27     | -0.34        | 1.2          |
| <b>ES~Wetland order</b>                                       |                 |           |          |          |              |              |
| intrcpt (Headwater Wetlands)                                  | 0.52            | 0.21      | 2.47     | 0.01     | 0.11         | 0.94         |
| factor(Floodplains)   | -0.44           | 0.5       | -0.88    | 0.38     | -1.43        | 0.54         |
| <b>ES~Study design</b>  |                 |           |          |          |              |              |
| intrcpt(Control-Impact)                                       | 0.43            | 0.23      | 1.89     | 0.06     | -0.02        | 0.89         |
| factor(Before-After/Control-Impact)                           | 0.04            | 0.44      | 0.1      | 0.92     | -0.83        | 0.91         |
| <b>ES~Flood event</b>   |                 |           |          |          |              |              |
| intrcpt(Natural)  | 0.45            | 0.21      | 2.18     | 0.03     | 0.04         | 0.85         |
| factor(Extreme)   | -0.01           | 0.73      | -0.01    | 0.99     | -1.44        | 1.42         |
| <b>ES~Study type</b>  |                 |           |          |          |              |              |
| intrcpt (Empirical)   | 0.22            | 0.25      | 0.89     | 0.37     | -0.27        | 0.71         |
| factor (Modelled)   | 0.55            | 0.44      | 1.26     | 0.21     | -0.3         | 1.41         |
| factor(Modelled from Empirical)                               | 0.5             | 0.6       | 0.84     | 0.4      | -0.67        | 1.67         |
| <b>ES~Wetland type</b>  |                 |           |          |          |              |              |
| intrcpt(SWDS+GWDS)  | 0.33            | 0.41      | 0.8      | 0.42     | -0.48        | 1.14         |
| factor(Surface Water Depression/Slope)                        | 0.00            | 0.56      | 0.00     | 0.1      | -1.09        | 1.09         |
| factor(Groundwater Depression/Slope)                          | 0.5             | 0.54      | 0.93     | 0.35     | -0.56        | 1.56         |
| factor(Floodplain)  | -0.25           | 0.62      | -0.39    | 0.69     | 1.46         | 0.98         |
| Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 |                 |           |          |          |              |              |

## **Appendix F. Description of each moderator and associated metadata for pollination services delivered by pollinator populations in agroecosystems.**

Although many studies described their systems as polycultures, pollination services were invariably inferred based on pollination indicators estimated for a single plant species, with one exception (Morandin and Winston 2005). For all but this study, effect sizes were associated with a single target plant species (crop). Morandin and Winston (2005) was therefore removed from any analysis involving plant attribute moderators.

Many earlier pollination studies (before the introduction of exclusion studies) estimated 'pollen removal efficiency' of pollinators. Most of these studies did not satisfy my study inclusion criteria because they have no control (i.e. sites or plots without pollinators) from which to infer pollination service provisioning. Moreover, estimates of pollen removal efficiency may be unrelated to actual pollination deposition. Several more recent studies measure pollen visitation, but the same problem arises (i.e. no control to permit estimates of effect size). In this case, natural pollinator populations acted as *potential* pollinators through pollen analysis but no data are presented that would allow one to infer that the natural pollinator made contact with anther and/or stigma. Therefore to be included, some indicator directly related to fertilization must be measured or estimated (e.g. growth of fruit over a period of time or a count of actual pollen deposited to the same or different flower).

### ***Agroecosystem descriptions***

The agroecosystem type (e.g. field, orchard, plantation, etc.) used to describe the site name or agricultural ecosystem was documented. Agroecosystems were defined by the number of distinct farms; number of sampling sites; site units (e.g. transect, plot); sampling unit size (in hectares); whether shade was a factor explicitly considered or manipulated in the study; whether it was a mixed system (i.e. included natural vegetation) or not; whether it was monoculture/polyculture or both; whether managed insect colonies/hives were used (and if so, the number of hives used); and sampling design/gradient. Also recorded were the description of natural habitat, different cultivars used and if culture types were

categorized based on shade levels. These three variables were too sparse and unsystematically reported in studies to be included in my analysis.

### ***Descriptors of pollinator visitation***

Most pollination studies use pollinator visitation surveys to estimate the diversity and abundance of pollinators. The only moderator used in the current analysis was whether pollinator visitation was used to infer the level of pollination service provisioning. The database includes information on a number of variables relating to the visitation surveys, including the timing of visitation surveys; time interval between successive surveys; the total number of sampling intervals; the duration of the entire sampling period; survey sampling units (transect, row, plot etc.); number of sampling units; size of units; average distance between sampling units; average number of plants per sampling unit, total number of plants surveyed; total number of flowers surveyed and additional methods (e.g. sweep netting, voice recording, pan netting etc.). None of these variables were included in my analysis because of their sparse and unsystematic reporting in published studies.

### ***Descriptors of the pollinator community***

For each study, I attempted to characterize the pollinator community on the basis of reported information. If reported, information was extracted on: richness of the pollinator community; pollinator abundance; whether pollinators were native or not, what proportion of pollinators which were native or introduced, whether pollinators could fly or not, whether pollinators were social or solitary, whether ants were included or not and the animal order in which pollinators belonged to.

### ***Plant***

As noted above, with the exception of one study, each study estimated the level of service provided by pollinators for a single target plant species, usually a commercial crop. For each study then, I extracted information (when reported on): Aside from the plant species used to measure pollination, several other plant attributes were analyzed:

- i) whether the target plant is herbaceous or woody,
- ii) whether the target plant bears fruit
- iii) whether the rewards for pollinators are nectar, pollen or oil
- iv) whether the target plant is commercial harvested
- v) whether the target plant is self-compatible
- vi) whether the target plant requires obligate outcrossing (cross pollination)  
whether pesticide was used
- vii) whether fertilizer was used
- viii) whether the target plant is known to benefit from the visitation of natural  
pollinator populations or not
- ix) whether the study mentions that buzz pollination was present
- x) and the mating system of flowers

**Appendix G. Model results of the predictor moderators showing bivariate influence on effect size when all effect sizes are analyzed (k=173).**

| <b>Model</b>                                 | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b> | <b>ci.lb</b> | <b>ci.ub</b> |     |
|--|-----------------|-----------|----------|----------|--------------|--------------|-----|
| <b>ES~Mixed</b>                              |                 |           |          |          |              |              |     |
| intrcpt (Not Mixed with Natural Vegetation)  | 1.23            | 0.1       | 12.07    | <.0001   | 1.03         | 1.42         | *** |
| factor(With Natural Vegetation)1             | -0.79           | 0.12      | -6.69    | <.0001   | -1.02        | -0.56        | *** |
| <b>ES~Pollination measurement indicators</b> |                 |           |          |          |              |              |     |
| intrcpt (Fruit Set)                          | 0.61            | 0.08      | 7.73     | <.0001   | 0.46         | 0.77         | *** |
| factor(Seed Mass)1                           | -0.12           | 0.14      | -0.9     | 0.37     | -0.4         | 0.15         |     |
| factor(Seed Set)2                            | -0.13           | 0.13      | -1.01    | 0.32     | -0.39        | 0.13         |     |
| factor(Fruit Weight)5                        | 0.45            | 0.31      | 1.46     | 0.14     | -0.15        | 1.04         |     |
| factor(Pollen Grains)6                       | -0.01           | 0.22      | -0.02    | 0.98     | -0.44        | 0.42         |     |
| factor(Pollen Efficiency/Deposition)7        | 1.38            | 0.24      | 6.08     | <.0001   | 1            | 1.96         | *** |
| <b>ES~Pollinator community attribute</b>     |                 |           |          |          |              |              |     |
| intrcpt (Abundance)                          | 0.39            | 0.08      | 4.82     | <.0001   | 0.23         | 0.55         | *** |
| factor(Richness)1                            | 0.07            | 0.13      | 0.53     | 0.59     | -0.18        | 0.32         |     |
| factor(Diversity)2                           | 0.71            | 0.32      | 2.21     | 0.03     | 0.08         | 1.35         | *   |
| factor(Presence/Absence-Exclusion)3          | 0.7             | 0.12      | 5.68     | <.0001   | 0.46         | 0.94         | *** |
| factor(Abundance and Richness)4              | 0.17            | 0.66      | 0.26     | 0.79     | -1.12        | 1.47         |     |
| <b>ES~Culture type</b>                       |                 |           |          |          |              |              |     |
| intrcpt (Monoculture)                        | 1.2             | 0.11      | 11.33    | <.0001   | 1            | 1.41         | *** |
| factor(Polyculture)1                         | -0.73           | 0.13      | -5.71    | <.0001   | -0.99        | -0.48        | *** |
| factor(Monoculture+Polyculture)2             | -0.79           | 0.16      | -4.96    | <.0001   | -1.1         | -0.48        | *** |
| <b>ES~Buzz</b>                               |                 |           |          |          |              |              |     |
| intrcpt (No Buzz Pollination)                | 0.58            | 0.05      | 10.94    | <.0001   | 0.48         | 0.69         | *** |
| factor(Buzz Pollination)1                    | 1.48            | 0.26      | 5.7      | <.0001   | 0.97         | 1.99         | *** |
| <b>ES~Year</b>                               |                 |           |          |          |              |              |     |
| intrcpt                                      | 56.18           | 10.46     | 5.37     | <.0001   | 35.68        | 76.68        | *** |
| data(Year Published)                         | -0.03           | 0.01      | -5.31    | <.0001   | -0.04        | -0.02        | *** |
| <b>ES~Hives</b>                              |                 |           |          |          |              |              |     |
| intrcpt (No Managed hives)                   | 0.51            | 0.06      | 8.25     | <.0001   | 0.39         | 0.63         | *** |
| factor(Managed Hives)1                       | 0.56            | 0.12      | 4.48     | <.0001   | 0.31         | 0.8          | *** |
| <b>ES~Pesticide use</b>                      |                 |           |          |          |              |              |     |
| intrcpt(no pesticide)                        | 0.62            | 0.06      | 11.31    | <.0001   | 0.52         | 0.73         | *** |
| factor(pesticide)                            | 1.94            | 0.54      | 3.57     | 0.0004   | 0.87         | 3            | *** |
| <b>ES~Herb</b>                               |                 |           |          |          |              |              |     |
| intrcpt(woody)                               | 0.84            | 0.08      | 10.4     | <.0001   | 0.68         | 0.1          | *** |
| factor(herbaceous)                           | -0.36           | 0.11      | -3.28    | 0.001    | -0.57        | -0.14        | **  |
| <b>ES~P_Native</b>                           |                 |           |          |          |              |              |     |

|  |       |      |       |        |       |       |     |
|--|-------|------|-------|--------|-------|-------|-----|
| intrcpt(mostly introduced)                                       | 1.01  | 0.12 | 8.16  | <.0001 | 0.77  | 1.25  | *** |
| factor(mostly native)  | -0.45 | 0.14 | -3.27 | 0.001  | -0.72 | -0.18 | **  |
| <b>ES~Commercial</b>   |       |      |       |        |       |       |     |
| intrcpt(not commercial)  | 0.25  | 0.14 | 1.8   | 0.07   | -0.02 | 0.53  | .   |
| factor(commercial)   | 0.46  | 0.15 | 3.01  | 0.003  | 0.16  | 0.76  | **  |
| <b>ES~Fruit</b>  |       |      |       |        |       |       |     |
| intrcpt(No Fruit)  | 0.38  | 0.11 | 3.33  | 0.0009 | 0.16  | 0.6   | *** |
| factor(Fruit)  | 0.35  | 0.13 | 2.66  | 0.008  | 0.09  | 0.6   | **  |
| <b>ES~Pvisit</b>   |       |      |       |        |       |       |     |
| intrcpt(pollinator visitation not used to infer)                 | 0.8   | 0.1  | 7.76  | <.0001 | 0.6   | 1     | *** |
| factor(pollinator visitation used to infer)                      | -0.22 | 0.12 | -1.78 | 0.08   | -0.46 | 0.02  | .   |
| <b>ES~Ants</b>   |       |      |       |        |       |       |     |
| intrcpt(Ant influence not measured)                              | 0.66  | 0.06 | 11.6  | <.0001 | 0.55  | 0.78  | *** |
| factor(Ant influence measured)                                   | -0.45 | 0.28 | -1.63 | 0.1    | -0.99 | 0.09  |     |
| <b>Significant Codes: 0 '***', 0.001 '**', 0.01 '*', 0.05'.'</b> |       |      |       |        |       |       |     |

**Appendix H. Model results of the predictor moderators showing bivariate influence on effect size when a subset of effect sizes are analyzed (k=112).**

| <b>Model</b>                                | <b>Estimate</b> | <b>SE</b> | <b>Z</b> | <b>p</b> | <b>ci.lb</b> | <b>ci.ub</b> |     |
|---|-----------------|-----------|----------|----------|--------------|--------------|-----|
| <b>ES~Pollination measurement indicator</b> |                 |           |          |          |              |              |     |
| intrcpt (Fruit Set)                         | 0.52            | 0.08      | 6.29     | <.0001   | 0.36         | 0.68         | *** |
| factor(Seed Mass)1                          | -0.24           | 0.16      | -1.53    | 0.13     | -0.56        | 0.07         |     |
| factor(Seed Set)2                           | -0.15           | 0.15      | -0.99    | 0.32     | -0.44        | 0.14         |     |
| factor(Fruit Weight)5                       | 0.54            | 0.28      | 1.95     | 0.05     | -0.001       | 1.09         | .   |
| factor(Pollen Grains)6                      | -0.23           | 0.32      | -0.72    | 0.47     | -0.87        | 0.4          |     |
| factor(Pollen Efficiency/Deposition)7       | 1.82            | 0.38      | 4.74     | <.0001   | 1.07         | 2.57         | *** |
| <b>ES~Buzz</b>                              |                 |           |          |          |              |              |     |
| intrcpt (No Buzz Pollination)               | 0.47            | 0.06      | 7.81     | <.0001   | 0.35         | 0.59         | *** |
| factor(Buzz Pollination)1                   | 1.9             | 0.44      | 4.32     | <.0001   | 1.04         | 2.76         | *** |
| <b>ES~Pesticide use</b>                     |                 |           |          |          |              |              |     |
| intrcpt(no pesticide)                       | 0.47            | 0.06      | 7.96     | <.0001   | 0.36         | 0.59         | *** |
| factor(pesticide)                           | 2.12            | 0.48      | 4.38     | <.0001   | 1.17         | 3.07         | *** |
| <b>ES~Mixed</b>                             |                 |           |          |          |              |              |     |
| intrcpt (Not Mixed with Natural Vegetation) | 1.09            | 0.19      | 5.78     | <.0001   | 0.72         | 1.47         | *** |
| factor(With Natural Vegetation)1            | -0.66           | 0.2       | -3.29    | 0.001    | -1.05        | -0.27        | **  |
| <b>ES~N_indvis</b>                          |                 |           |          |          |              |              |     |
| intrcpt                                     | 0.41            | 0.07      | 5.79     | <.0001   | 0.27         | 0.55         | *** |
| data(N_indvis)                              | 0.0001          | 0         | 2.9      | 0.004    | 0            | 0.0002       | **  |
| <b>ES~Sociality</b>                         |                 |           |          |          |              |              |     |
| intrcpt (solitary)                          | 0.4             | 0.12      | 3.22     | 0.001    | 0.16         | 0.64         | **  |
| factor(social)                              | -0.35           | 0.23      | -1.54    | 0.13     | -0.8         | 0.1          |     |
| factor(social and solitary)                 | 0.24            | 0.15      | 1.6      | 0.11     | -0.06        | 0.6          |     |
| <b>ES~Pollinator community attribute</b>    |                 |           |          |          |              |              |     |
| intrcpt (Abundance)                         | 0.33            | 0.09      | 3.6      | 0.0003   | 0.15         | 0.51         | *** |
| factor(Richness)1                           | 0.17            | 0.14      | 1.22     | 0.22     | -0.11        | 0.45         |     |
| factor(Diversity)2                          | 0.77            | 0.31      | 2.47     | 0.01     | 0.16         | 1.39         | *   |
| factor(Presence/Absence-Exclusion)3         | 0.41            | 0.16      | 2.54     | 0.01     | 0.09         | 0.72         | *   |
| factor(Abundance and Richness)4             |                 |           |          |          |              |              |     |
| <b>ES~Commercial</b>                        |                 |           |          |          |              |              |     |
| intrcpt(not commercial)                     | 0.25            | 0.16      | 1.63     | 0.1      | -0.05        | 0.6          |     |
| factor(commercial)                          | 0.3             | 0.17      | 1.77     | 0.08     | -0.03        | 0.64         | .   |
| <b>ES~Fruit</b>                             |                 |           |          |          |              |              |     |
| intrcpt(No Fruit)                           | 0.28            | 0.15      | 1.93     | 0.05     | -0.004       | 0.57         | .   |
| factor(Fruit)                               | 0.28            | 0.16      | 1.72     | 0.09     | -0.04        | 0.59         | .   |

**ES~St\_Design**

|              |       |      |       |        |       |      |     |
|--------------|-------|------|-------|--------|-------|------|-----|
| intrcpt (CI) | 0.71  | 0.12 | 5.74  | <.0001 | 0.46  | 0.95 | *** |
| factor(BACI) | -0.27 | 0.14 | -1.88 | 0.06   | -0.55 | 0.01 | .   |

**ES~Hives**

|                            |      |      |      |        |       |      |     |
|----------------------------|------|------|------|--------|-------|------|-----|
| intrcpt (No Managed hives) | 0.46 | 0.07 | 6.74 | <.0001 | 0.33  | 0.6  | *** |
| factor(Managed Hives)1     | 0.29 | 0.17 | 1.66 | 0.1    | -0.05 | 0.62 | .   |

**ES~Culture type**

|                                  |       |      |       |        |       |       |     |
|----------------------------------|-------|------|-------|--------|-------|-------|-----|
| intrcpt (Monoculture)            | 0.99  | 0.24 | 4.09  | <.0001 | 0.51  | 1.46  | *** |
| factor(Polyculture)1             | -0.49 | 0.15 | -1.91 | 0.06   | -0.98 | 0.01  | .   |
| factor(Monoculture+Polyculture)2 | -0.57 | 0.27 | -2.13 | 0.03   | -1.09 | -0.04 | *   |

**Significant Codes: 0 '\*\*\*', 0.001 '\*\*', 0.01 '\*', 0.05'."**