This manuscript was previously submitted to *Food Webs* as Ms. Ref. No.:  FOOWEB-D-14-00006. The new version includes a rewritten and reorganized methods section, as well as more easily interpretable figures. Below we outline the points made by the editor and two reviewers (regular font) and our responses to those comments (in bold).

**Editor’s comments**

1.      Please include a graphical abstract and Highlights section. See <http://www.elsevier.com/journals/food-webs/2352-2496/guide-for-authors#40010> for details. **Done**  
2.      Use "and", not "&" for references, e.g. Pimm and Lawton 1977 (lines 17-18). **Done**  
3.      Groups of references should be listed first alphabetically, then chronologically. Line 18, for example, should be (Pimm 1982; Yodzis 1981). **Done (but double check this**  
4.      Please expand the abstract. It is currently relatively short and I believe a few additional sentences will aid in clarifying the scope/scale of the research undertaken. **Edited and added some clarifying points.**   
5.      Please replace 1, 2, 3, 5 (lines 19, 20, 21, 26) with one, two, three and five.  **Done**  
6.      Last sentence of the first paragraph of the introduction should be deleted and this should be discussed later in the paper (Discussion). **Deleted** There are numerous other places in the introduction with text out of place (Reviewer #1 brings this up). It would help the readability of the introduction if this section of the paper did not move between results, interpreting your results. Please read through carefully and tease apart the sentences that are not necessary and either remove them from the manuscript or move them to the discussion and expand if/when necessary. **We edited the introduction to have better flow, and eliminated results.**   
7.      Delete "; 253" on lines 35-36. It is not necessary. Reviewer #1 wants this part deleted and I can see their point. In order to keep it in the paper, further integration is necessary. I would also benefit the paper by expanding the introduction in places, as suggested by reviewers. **Removed it**  
8.      Line 41, add "a" between "at" and "trophic".  **Done**  
9.      Figure 1b is not mentioned until the results (line 201). I would therefore request this be a separate figure inserted at the appropriate place in the manuscript. **The figure has been revised**  
10.     Delete comma at end of line 57. **Done**  
11.     Please have one section for Methods (2. Methods). Then 2.1 Model Selection will be a sub-heading, 2.2 Simulation models, 2.2.1 Sensitivity analysis. **Done**  
12.     Not necessary to refer to specific page numbers of papers (e.g. lines 141, 143). **Deleted**  
13.     Unless I missed it, there is no reference to Figure A2 in the text. Please carefully go through the text and make sure all figures, appendices etc, are referred to correctly and in the appropriate order.  **There is reference to the figure, it is now Figure 2**  
14.     Please follow Journal format for references. For example: "Van der Geer, J., Hanraads, J.A.J., Lupton, R.A., 2010. The art of writing a scientific article. J. Sci. Commun. 163, 51-59."  
15.     Please do not capitalize all letters in figure axes labels. **Done**  
16.     Please add reference to Appendix A in the legend of Figure 1 to direct readers to the literature used to form this figure. **Added reference to the Appendix for all figures to direct readers to how the figure was generated.**

**Reviewer 1 comments**

One issue I have with this paper is that the author's don't really clarify what they mean exactly by a "food chain". They seem to use this term interchangeably with the number of trophic levels in a food web, but is this what they meant? For example, couldn't a food chain have a series of horizontal steps within the same trophic level, such as an herbivore feeding on a plant, a spider feeding on the herbivore, a bigger spider feeding on the first spider, a bigger spider feeding on the second spider, etc (with each spider considered a member of the third trophic level). This is a crude example but would the horizontal steps in the third trophic level (i.e., the predators) mean there are five links in the food chain but only three trophic levels. I think the authors need to better define their terminology up front and distinguish the relationships they want to imply between food chain length and trophic levels in a food web (are these the same, different, etc?)

**We clarified the definitions used in this manuscript in the first paragraph of the introduction. In the reviewer’s example this would, topologically, constitute a food chain with 5 trophic levels based on our definitions.**

The introduction of this paper is extremely poorly written. There often seems to be little connecting one paragraph to the next, and the authors discuss their results in seemingly every paragraph without even describing what their study is going to do. I had a very hard time following the line of thought as it just seemed like a jumble of different ideas, without any linear flow that made sense.

**Deleted some out of place sentences and added some connecting thoughts.**

The model is not explained in suitable fashion. The first sentence of the model selection paragraph describes a sign matrix generated for each food web, without even talking about what types of food webs were generated. Shouldn't this be the first thing that the authors discuss? Moreover, assumptions are not clearly defined. What is the predator-dependent functional response and how is it modeled? Similarly, terms like prey-dependence and ratio-dependence will not be clear to all readers and need a definition. I honestly read to the end of line 156 and have absolutely no idea what the authors actually did with this model.

**The new version of the manuscript features a rewritten and reorganized methods section that should be clearer. In this case the particular form of the functional response is not relevant to the study, just the predictions that follow from predator-dependent functional responses in general and how that impacts the magnitudes of the elements of the Jacobian matrix. We explain this in the Model Assumption section of the paper.**

The results of the simulations seem to contradict the empirical data, which was a flaw pointed out by the authors in the introduction. They mention that stability declines significantly from 3 to 4 trophic levels (L202-203). But, looking at Figure 1A food webs with this many trophic levels appear to be about equally likely in nature. Can they explain this discrepancy? I would expect (based on the empirical data) a big drop off from 2 to 3 and a similarly large drop off from 4 to 5.

**Part of the confusion here is that the binwidths of the histogram were not properly set. This issue has been fixed, and each bin now corresponds to a full trophic level, that is all species with a trophic position greater than or equal to two but less than three for example. Additionally we would not expect the data to exactly match the empirical data in this case as a result of our simplifying assumption of universal omnivory in what we are now calling our “simple webs.” Our goal here is simply to show that the declining trend in species with a high trophic position is coincident with a negative relationship between quasi sign-stability and chain length. The new organization and figures should help to clarify this point.**

The authors point on L245-246 is a key one. In Nature food chains are embedded in complex webs. However, their simulation model only assumed ten species. The results would be more convincing if the food webs they simulated were more representative of real-world food webs (i.e., potentially hundreds of interacting species). I realize this may be computationally unfeasible (perhaps) but a 10-species food web is far too simplistic to draw any real conclusions about what might operate in nature.

**Ten species is substantially complex. The study of smaller community modules is a commonly accepted practice throughout community ecology. Even with only ten species we still have more complexity than the previous two studies on this topic (Pimm and Lawton 1977, Sterner et al. 1997). To complete this same analysis on webs of several hundred species would be too computationally intensive.**

Other issues/comments:  
  
L18-20: This is a bit misleading in my opinion. Looking at the figure 1A it seems there is relatively no difference between 3 and 4, thus this sentence should say that most species have a trophic position from 2 to 4. This is a problem because the trend does not line up with the simulation results.

**We changed the wording in the paragraph to quantitative descriptions of the proportions of species below a given trophic position so this should be clearer now. We further amended the figure to better represent the distribution of trophic positions.**   
  
L28-29: This seems like an odd ending to the first paragraph of the introduction. Such sentence, with evidence for how results compare to the perspectives paper, belong in the discussion not here.

**Deleted.**   
  
L30-31: This needs to be developed much more fully in my opinion. What are the predictions from each of (1) energetics; (2) foraging theory; and (3) dynamic constraints that suggest food chains should be constrained? Without explanation it's not clear what the strengths and weaknesses of each hypotheses are (which should also be explained, L31-32). It seems like the authors begin to develop these ideas in the third paragraph, such that the Macarthur quote seems completely out of place.

**These alternative hypotheses have been thoroughly discussed elsewhere. We also contend that the purpose of this paper is not to illuminate the issues with the different hypotheses, merely enlightening the reader that there have been other hypotheses that have been previously proposed. Furthermore, the main point of this part of the introduction is just to introduce the fact that most of these hypotheses have conflicting support.**   
  
L35-38: This quote has nothing to do with developing a broad introduction and should be deleted. Similarly, L38-39 is discussion not introduction.

**Deleted**  
  
L61-62: Again, the authors should not be ending introduction paragraphs with brief segments describing the implications of their results. It's hard to process the results of this paper before the authors even describe what they plan to do.

**Deleted**  
  
L93-94: The authors use a lot of jargon, but I point it out here. What is a sign-stable system? What is a trophic loop? These terms need to be defined.

**We have made an attempt to define all terms that may be confusing. For the two that have been pointed out, sign-stability is defined in XXX, and we have added a note giving an example of a trophic loop.**   
  
L122-123: I think the authors have ignored a major aspect of many food-webs, intra-guild predation. This can occur if predators eat other predators, or if herbivores eat other herbivores (which can occur passively if one herbivore eats plant tissue containing eggs of another). I find this omission problematic in that these interactions have shown to strongly affect community structure and ecosystem functioning. Not considering horizontal interactions within a trophic level is a major flaw in the reasoning of this paper.

**Intra-guild predation is explicitly included in the food webs we examined. We now mention this in the main text. Topologically intra-guild predation is defined when a predator eats a species that eats another prey item of that predator (A eats B, C eats A and B). we understand that there may be some confusion on this point in that we have referred to this phenomenon as omnivory, because in the given example here, where C is the intraguild predator, C and A have different trophic positions. Thus in our simple webs all species participate in intraguild predation. Intraguild predation is also allowed in food webs that we constructed using a random and niche model approach. It has also been shown that the niche model produces webs with similar numbers of intraguild predation modules as real food webs.**   
  
L124: Is the meaning that a predacious mammal could never eat an herbivore and a plant? This is obviously not the case, what about a bear for example (that would eat both a hare and plants the hare feeds on).

**We removed the hyperbole in this paragraph.**   
  
L142-143: What does donor-controlled mean?

**Donor control, as defined in the main text, relates to when there is no impact of an increase in the predator population on the prey population.**   
  
L158-159: Is this a method or a result?

**This is a method, albeit poorly worded. This issue has been fixed in the new methods section.**   
  
L160: Never use "as well as" unless it is a comparison (John could not play ball as well as Steve). Otherwise "and" is grammatically correct.

**Switched it to “and”**

**Reviewer 2 comments**

The authors do not mention another kind of explanation for limitation on food chain length that has been imposed, which has to do with colonization-extinction dynamics; basically, there is an inherent asymmetry in any food webs that involve specializastion (and all do, to some extent), in that say a herbivore cannot colonize unless its required plant is present, but the reverse is not true.  Moreover, if predators tend to drive their prey extinct, they can still nevertheless persist in a spatial context.  This has been known since the classic work of Huffaker in the 1950's; he experimentally showed that unstable predator-prey interactions leading to local extinction could persist in a spatial array of patches if dispersal is limited.   This involves another kind of dynamic constraint on food webs, having to do with spatial dynamics, in effect overriding local instability.   The spatial hypothesis of Post et al. (see also papers by Holt, like book chapter in  
Losos-Ricklefs) is itself for the most part a 'dynamical constraints' hypothesis.

**We have made reference to alternative dynamics based hypotheses in both the introduction and discussion.**

I found the arrangement and formatting of figures and legends very annoying.  Please put figures like A1 and A2 in the main text, and put each figure directly with its legend.  It is hard to fully understand what the text says without inspecting these figures, so put them in the main text.  And, the code can all be compiled and annotated separately.  For sure put that (the code) in the appendix.  
The figures verge on being unreadable, at least in my copy.

**The figures previously in the Appendix are now in the main manuscript. Appendix A now just contains data citations and code.**

The flow of thoughts in the paper in describing and justifying the model is a little unclear, and should be clarified and strengthened.   The authors on lines 12-129 state that they will deal with a model with "universal omnivory". So if one ranks-order species, the top-ranked species is eaten by no one, but it eats all other species; likewise, a species of rank n eats all species with lower rank.  Is this correct?  If so, say it.  They should explicitly note how this limiting case differs from (or is similar to) models such as Cohen's cascade model, and subsequent niche models of Martinez, Williams, and others.

**We have added to the methods section a paragraph describing our justification for using the random model. For comparison we have also added a new section that analyzes webs constructed based on the niche model.**

 It really is not obvious to me that universal omnivory is more "realistic" than assuming linear unbranched chains.  If one takes into account the actual heterogeneity of weightings of flows and interactions in a matrix, and tossed quantitatively negligible links, there would be much less omnivory than assumed here.

**Looking at a set of ecosystem flow networks provided by Ulanowicz that include flow weights it seems as if there is no decrease in omnivory when you only look at the subset of the web that includes the top 50% of weights/interaction strengths. We have added a new section to the Appendix to show this.**

The whole protocol of the paper is to assess the local stability of equilibria in randomly assembled matrices with specified constraints.  The authors need to say something about what happens when an equilibrium is unstable.  Do you expect species to always go extinct, without oscillations?  The simplest example of this is the 2-species Lotka-Volterra model, where with stronger inter than intraspecific competition, an equilibrium with both species present exists, but the slightest deviation leads to one or the other winning out (the priority effect case).  Or instead, are there sustained oscillations around the equilibrium. I realize their protocol breaks down, but systems deemed unstable could nonetheless persist, but with oscillations.  Maybe systems with long chains are actually persisting, just not at a stable local equilibrium.

**This is not the main focus of the paper, we merely suggest that webs that are more likely to be stable over a large range of parameters would be more likely to persist in a changing environment without altering the structure. It is possible that webs with low quasi sign-stability can persist in nature if they are quantitatively stable, or through spatial dynamics. We have expanded the discussion to include this possibility.**

In the case of Lotka-Volterra models, these oscillations can for instance be heteroclinic, which would imply deviations to such low numbers that extinction is still highly likely.  So there still could be a dynamical constraint on food chain length. Is that what happens with these nearly donor-controlled systems, which include strong predator interference?   I would like the authors to provide a better analytical understanding for why instability occurs, and when it actually leads to extinctions, say working it out for a small number of cases. With 3 species, there are three Routh-Hurwitz criteria that need to be satisfied, for local stability, maybe just one of them gets violated when things go unstable.  The dimensionality of the system is low enough that Levins' loop analysis approach could shed some insight into what is happening.   In other words, for at least this limiting case, lay out more clearly the forces at work in the 'dynamical selection' that may be limiting food chain length a bit even with 3 species.

**The reviewer here raises a very interesting point, but we believe that this is beyond the scope of the current paper. It seems as if this topic would be worthy of a paper unto itself, especially since the three species example is only a relatively small part of a much larger sample of webs. It is not clear that understanding the three species case would greatly enhance our understanding of the general case.**

 After you create your 'universe' of possible food webs, each with a corresponding matrix your stability criterion in effect cleaves this class of matrix into two subclasses, one with eigenvalues permitting local stability, the other not.  Are there any obvious patterns in the strength of interactions in these matrices, for instance, that would explain the difference?  Maybe the unstable ones all have on average higher interaction strengths.

**There was no obvious pattern in the subset of interaction strengths that yielded a stable matrix. Sampled values in stable matrices were relatively uniformly distributed throughout the sampling distributions. We chose not to include this in the final manuscript as a result.**

Universal omnivory is one limiting case.  Another that seems to be embedded in your model would be pure donor control, where the predators have no impact on their prey at all.  But the eigenvalues of a block triangular matrix is just the set of its diagonal elements, which in your case are by assumption all equal to -1.  So in that limit, as you mention, all food chains of any length in your model would be stable!  So the limit to food chain length you observe in your simulations, must somehow essentially have to do with deviations away from donor control.  You need to reflect on the mechanistic underpinning of your results a bit more.  
Thinking this through is I think important for understanding your results.

**We agree that donor control would be a limiting case as well. This is discussed in the Model section of the paper. The importance of deviations from pure donor control is explored in the discussion of the impact of different distributions used to sample values for the Jacobian matrix. As we note it seems as if it is important that there be a small deviation, meaning that there is asymmetry in the relative impacts the predators and prey have on each other. When distributions are symmetrical, however, the pattern disappears.**

Section 3.1 is titled "Sensitivity analysis".  I think this phrase is often used in a more narrow sense than this.  Were one examining a matrix projection model, sensitivity analysis would be an analysis of how eigenvalues change with small changes in each entry of the matrix.  Here  you are doing  something broader, varying connectivity, asymmetry, etc.  Maybe call this "steps towards robustness" or something along those lines.

**With the new organization of the manuscript this section is more aptly titled.**

It seems to me that the two parts of Figure 1 report different things.  The figure on the left is the distribution of the trophic position of species, which is not the same as the number of trophic levels within a community (which is what is shown on right).  So the same label is used for the two abscissa, when actually they are quite different.  What happened to species at level 1?  There must be something down there!

**Changed the figure to be more accurate**

In looking at the suite of figures as a whole, a pattern that is considerably stronger than the food chain length result, is the overall great decline in likely QSS with increasing number of interactions.   So 'dynamical selection' should be culling out communities with high interaction density.  The authors should discuss this.  Maybe there is 'selection' on the overall richness of interactions, and the effect on food chain length is a kind of correlated by-product.

**This is not altogether a surprising result, as May (1972) found that increasing connectance, interaction strength, and number of species will influence the stability of communities. We have added a brief section discussing the implications of selection against highly connected webs.**

Minor to medium points:  
Line 19. State whether species with no prey, are at position 0 of 1  **Done**  
Line 23.  In Figure A1 (which as noted above should be in main text), there are actually more webs with a maximal chain length of 6, than with 3, so you should write something like "between 3 and 6"  **Changed to a more quantitative description based on percentages.**   
Line 56. No comma after "levels". **Done**  
Line 65.  "four species food chains" should be "four-species food webs"; Pimm and Lawton include some examples with omnivory, hence not simple, unbranched chains. **Done**  
Line 97.  I think a hyphen is needed after "quasi". **Perhaps, but in Allesina and Pascual 2008 (the paper introducing the concept) they did not include one and we chose to keep it as they wrote it**  
Lines 123-124. Using "chains" seems odd here.  Replace with "webs".  On next line thought about lynx etc. should be put in parentheses. **Done**  
Lines 149-150.  "positive values on one side…"  I really do think   this seems biologically quite implausible.  The authors need to provide some references or additional arguments that this limit is not totally unrealistic.  
Line 159.  If this figure is not in printed version (and I think it should be), then you will need a more clear description in text to describe what you are doing. **Figure is now in the main article**  
Line 163.  Put the phrase "an independent" before "random".  **Done**  
Lines 186-187.  The whole text in this section is hard to follow.  I would be hard-pressed to replicate what the authors have done.  Shouldn't some of the entries be negative, as well as the positive 1's, since these are predator-prey interactions?  Do the number of interactions on 187 refer to predator-prey interactions (direct interactions).  So for a 10 species unlinked chain, there are 9 predator-prey pairs, and one might select 3 additional omnivory pairs from these?  So higher connectance implies more omnivory?

**This is outlined better in the new manuscript. The idea here is that we first generated the adjacency matrix of the food web, and then converted this into the sign matrix (a one at *aij* is a stand in for a positive at *aij* while *aji* would then be filled with a negative value. We understand that this was confusing as written and think that the new version is clearer.**

Lines 190-191.  So there were 1000 random draws for each of the 40,500 food webs? **Yes, but we have made some small changes that we think have simplified and clarified this section.**   
Lines 196-198.  I assume you mean you found the eigenvalue with the largest real part. **Yes, we fixed this.**   
Line204.  Add a comma after "species". **Yes**  
Line 208. Replace commas with parentheses, around "Figure 2"  **Done**  
Line 215.  The effect of an increase in quasi sign stability seems rather minor, so add a word like "slightly".  **Done**  
Line 230.  Say "number" not "numbers". **Done**  
Line 234. Insert "non-basal" before "species". **Done**  
Line 254.  The 24 and 28 interactions are not shown in Figure 2, but instead in Figure S3 etc.  Are these figures basically the same? **Yes this was done for clarity. We have altered the way the data will be displayed in new figures that enable the reader to better see the patterns, without having to squint at overlayed combinations.**