

Coevolution leaves a stronger imprint on interactions than on community structure

Timothée Poisot and Daniel B. Stouffer

School of Biological Sciences, University of Canterbury,
Christchurch, New Zealand

1 Coevolutionary dynamics act on both species and their interactions in
2 ways that shape ecological communities ^{1–4}. It remains unclear, how-
3 ever, how the structure of communities at larger spatial scales either
4 influences or is influenced by local coevolutionary processes ^{5,6}, and how
5 mechanisms acting at these different scales feedback onto one another
6 ^{7–9}. Here we show that, although species interactions vary substantially
7 over a continental gradient, the coevolutionary significance of individual
8 interactions is maintained across different scales. Notably, this occurs
9 despite the fact that observed community variation at the local scale
10 frequently tends to weaken or remove community-wide coevolutionary
11 signal. When considered in terms of the interplay between community
12 ecology and coevolutionary theory, our results demonstrate that indi-
13 vidual interactions are capable and likely to show a consistent signature
14 of past coevolution even when woven into communities that do not.

15 Ecological interactions often exert important selective pressures on the species in-
16 volved. For example, the phenologies of lodgepole pines and red crossbills respond

1 spatially to the presence of squirrels ¹ and palm species undergo changes in seed
2 morphology in response to the extinction of bird dispersing their seeds ³. Given
3 that interactions are distributed in similar ways across communities, at both the
4 large or small scale ¹⁰, it can be argued that much ecological structure is the end
5 result of evolutionary or coevolutionary dynamics between species ^{11,12}. Unfortu-
6 nately, while the coevolutionary dynamic of pairs of interacting species has been
7 well described at macro ¹³ and micro ¹⁴ evolutionary timescales, most attempts
8 to understand how they cascade up to the levels of diversity of both species and
9 interactions found within empirical communities have been inconclusive ¹⁵. More-
10 over, because coevolutionary dynamics are often presented as a key driving force
11 behind ecological structure across both time and space ⁶, it is crucial to determine
12 the scale at which they are both relevant and quantifiable.

13 Historically, the evidence for coevolution in taxonomically diverse communities
14 is quantified as the degree of matching between the phylogenies of two sets of
15 interacting organisms ¹⁶. This notion builds on the century-old idea that extant
16 species interact in a way similar to the way their ancestors did ¹⁷, but it is consid-
17 erably more restrictive than just phylogenetic conservation of species' interactions
18 ^{11,18} because it additional higher-order constraints. More explicitly, communities
19 that have assembled by successive divergence events due to coevolution should
20 display phylogenetic congruence, that is (i) have similar phylogenetic trees and
21 (ii) have species at matching positions in the trees that tend to interact ⁷. On
22 the other hand, many ecological and evolutionary processes that occur locally are
23 expected to blur community-wide coevolutionary signal ⁹. One possible explana-
24 tion is that interactions can display substantial turnover at ecologically relevant
25 temporal and spatial scales ¹⁹: the same two species can interact in different ways

1 under the effect of local environmental contingencies, spatial mismatch in species
2 phenologies, variations in population abundances, and chance events ²⁰. It is un-
3 clear, however, whether these mechanisms influence how the coevolutionary signal
4 within individual interactions should vary across spatial scales.

5 To answer these questions, we study a dataset of interactions between rodents
6 and their ectoparasites from 51 sites across Western to Eastern Europe ²¹ (Meth-
7 ods Summary). This dataset is uniquely suited for this task as it represents
8 a paradigmatic system in which species-species interactions are thought to be
9 driven by macro-evolution and co-speciation events ²², and coevolutionary signal
10 is indeed significant at the continental level ²³ ($p \leq 10^{-4}$; Methods Summary).
11 Importantly, it also provides spatial replication and variability at a scale large
12 enough to capture macro-ecological processes.

13 As host-macroparasite interactions are hypothesized to be both ecologically con-
14 strained and evolutionary conserved ²⁴, the congruence observed at the continen-
15 tal level sets the baseline for what would be expected in local communities. Of
16 course, if ecological mechanisms reduce coevolutionary signal, we should detect
17 coevolution at the continental scale but not locally. Noting that variation of in-
18 teractions can decrease congruence, we analyse the data at two different levels to
19 test these hypotheses: first, we use *regional* interaction data—which accounts for
20 different species composition across sites—and second, we use the *local* interaction
21 data—which also accounts for variation in the interactions between observed these
22 species (Methods Summary). Out of 51 sites, 35 show no signal of coevolution, 11
23 show significant coevolutionary signal when using the regional interactions, and
24 12 show significant coevolutionary signal using the local interactions (see *Supp.*

1 *Mat. 1* for network-level significance values).

2 These results would appear to support the idea that macro-evolutionary processes
3 such as co-diversification can have consequences at the macro-ecological level but
4 may not in fact be detectable at finer spatial scales. On the other hand, system-
5 level differences say little about the behaviour of individual interactions, despite
6 the fact most coevolutionary mechanisms act at the interaction level ²⁵. As might
7 be expected, we observe here that networks with interactions that are important
8 for coevolution at the continental scale indeed have more coevolutionary signal at
9 the local and regional scales alike (Fig. 2A). Intriguingly, we also find that the
10 distribution of individual interactions' contributions to coevolution is strongly
11 conserved, regardless of the scale at which the interactions are quantified (Fig.
12 2B). Because interactions differ in their total contribution to coevolution, this
13 implies that their distribution across networks is what actually drives differences
14 in overall coevolutionary signal. Network-level coevolutionary signal emerges di-
15 rectly from the properties of interactions and is not a property of the network
16 itself.

17 Beyond their contribution to coevolution, interactions also ultimately differ in
18 how frequently they vary when the species involved co-occur ²⁶. Once more, the
19 literature on host-parasite interactions usually assumes that the reason why some
20 interactions are more frequent is because they reflect a significant past history
21 of coevolution ²⁷. If this were true, we should observe a significant, positive
22 correlation between the probability of observing an interaction and the importance
23 of that interaction for coevolution at the continental scale (Methods Summary).
24 Surprisingly, we find that neither is true here since interactions that are important

1 for coevolution are not more conserved (Fig. 3).

2 Ultimately, coevolutionary signal varies across scale because of the simultaneous
3 variation of species' interactions *and* communities' phylogenetic tree structure. In
4 a system characterised by substantial turnover, we would expect the contribution
5 of each separate interaction to differ across scales as well. Instead, we observe here
6 that interactions that contribute strongly to coevolutionary signal at the conti-
7 nental scale *also* show a significant tendency to contribute strongly at the local
8 scale (Fig. 4). Remarkably, this result implies that the remnants of coevolution
9 are still locally detectable in *individual interactions* even though coevolution fails
10 to leave its imprint on most local networks.

11 Overall, the results of our analyses demonstrate that there is a sizeable gap be-
12 tween our current understanding of coevolution as the basis of multi-species in-
13 teractions and its applicability to ecological questions. Local networks show little
14 to no signal of coevolution and the strength of coevolution between two species
15 is a surprisingly poor predictor of how frequently they interact. In contrast to
16 the frequent assumption that phylogenetic structure is a key driver of community
17 structure ²⁸, these data reveal that this impact is actually minimal at ecologi-
18 cally relevant spatial scales. Despite all the above, individual interactions are
19 able to maintain their coevolutionary signal even when the community they are
20 woven into does not. Thinking more broadly, these discrepancies provide a clear
21 roadmap for bridging the aforementioned gap between our appreciation of the role
22 of coevolution and its empirically measurable outcomes. Network structure is the
23 most parsimonious *mechanism* by which coevolution proceeds, not the imprint
24 coevolution leaves on ecological communities.

1 Methods Summary

2 We use data on observations of interactions between 121 species of rodents and
3 205 species of parasitic fleas in 51 locations across Europe ²¹ to build 51 species-
4 species interaction networks. Interactions were measured by combing rodents for
5 fleas, a method that gives high quality data as it has a high power of detection. To
6 account for differential sampling effort and across site variations in abundance, we
7 only study the networks' incidence matrices (presence and absence of interactions).

8 In our study, we define three scales for the network data and analysis—continental,
9 regional, and local. The continental scale is the aggregated “metanetwork” which
10 includes all potential interactions between co-occurring species ¹⁹ (*i.e.*, all species
11 and all their interactions across the 51 networks). Within each site, the regional
12 scale is given by the list of observed species and all their possible interactions.
13 Hence the regional networks are always a perfect subset of the continental net-
14 work. The local scale includes only the interactions that were actually observed
15 in the field at a given site. Therefore, the local and regional networks always
16 include the same species, but the local network has only a subset (or, at most, an
17 exact match) of the interactions in the regional network. The spatial consistency
18 of every individual interaction is measured as the number of sites in which the
19 two species involved co-occur.

20 We quantified the coevolutionary signal in terms of the degree of matching be-
21 tween host and parasite phylogenies given knowledge of species interactions using
22 the *PACO* method ²⁹, which is robust to variations in number of species. *PACO*
23 provides measures of both the network-level congruence (*i.e.*, is the network co-
24 evolved?) and the interaction-level signal (*i.e.*, what is the contribution of each

1 interaction to the overall coevolutionary signal?). We measured the phylogenetic
2 dissimilarity between two sites for hosts and parasites using PCD³⁰, a measure
3 that accounts for the dissimilarity of species, corrected for the phylogenetic dis-
4 tance between all species in the dataset. Since it is a requirement of the methods
5 we use here, the phylogenetic trees for hosts and parasites were rendered ultra-
6 metric (i.e., all species are at the same distance from the root).

7 References

8 **Acknowledgements.** We thank Juan Antonio Balbuena for discussions about
9 the *PACo* method, and members of the Stouffer and Tylianakis groups for com-
10 ments on an early draft of this manuscript. Funding to TP and DBS was provided
11 by a Marsden Fund Fast-Start grant (UOC-1101) and to DBS by a Rutherford
12 Discovery Fellowship, both administered by the Royal Society of New Zealand.

13 1. Benkman, C. W., Parchman, T. L., Favis, A. & Siepielski, A. M. *et al.* Reciprocal
14 selection causes a coevolutionary arms race between crossbills and lodgepole pine.
15 *Am. Nat.* **162**, 182–194 (2003).

16 2. Thompson, J. N. *et al.* The coevolving web of life. *Am. Nat.* **173**, 125–140
17 (2009).

18 3. Galetti, M. *et al.* Functional Extinction of Birds Drives Rapid Evolutionary
19 Changes in Seed Size. *Science* **340**, 1086–1090 (2013).

20 4. Nuismer, S. L., Jordano, P. & Bascompte, J. *et al.* Coevolution and the Archi-
21 tecture of Mutualistic Networks. *Evolution* **67**, 338–354 (2013).

22 5. Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R. *et al.* Coevolution between

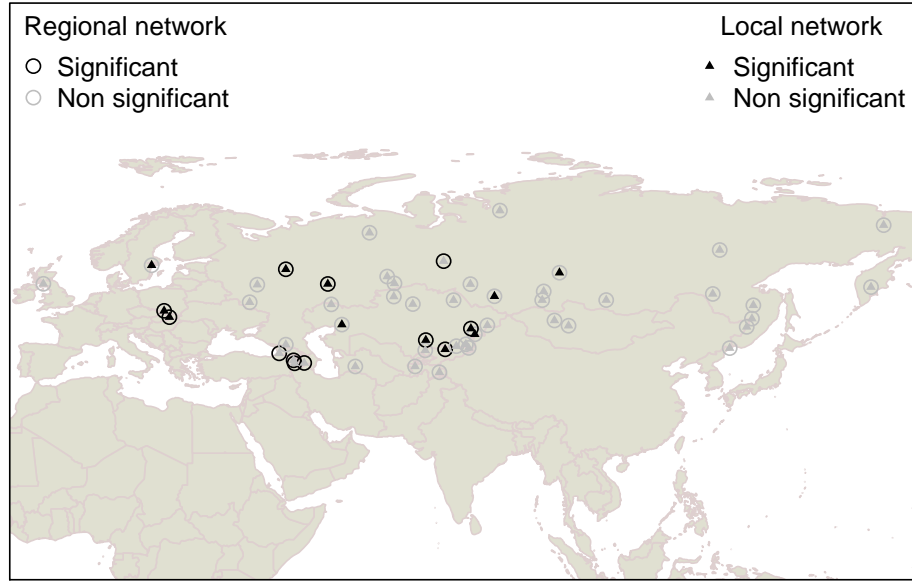


Figure 1: Spatial distribution of coevolutionary signal across the 51 sites. For each location, we indicate whether or not the structure of regional and local interaction networks is consistent with phylogenetic congruence. The colour of the circle corresponds to regionally significant or non-significant (black and grey, respectively) while the colour of the symbol within corresponds to locally significant or non-significant (black and grey, respectively).

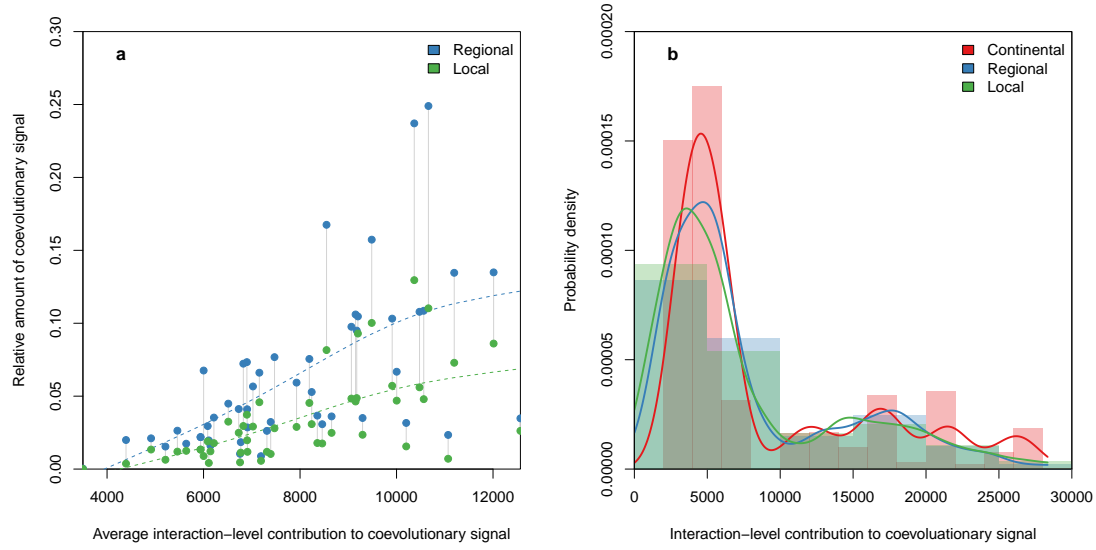


Figure 2: Distribution of coevolutionary signal at the network and interaction levels. **a**, Networks that have lower coevolutionary signal at the local or regional level are composed of interactions that on average contribute little to coevolution at the continental scale. Dashed lines are the cubic smoothing spline; the two levels of the same networks are linked by solid grey lines. **b**, Overall, interactions observed at the local, regional, and continental scale have equal contributions to coevolutionary signal. Probability density was smoothed using a Gaussian kernel density estimator. Raw probability densities are shown as semi-transparent bars.

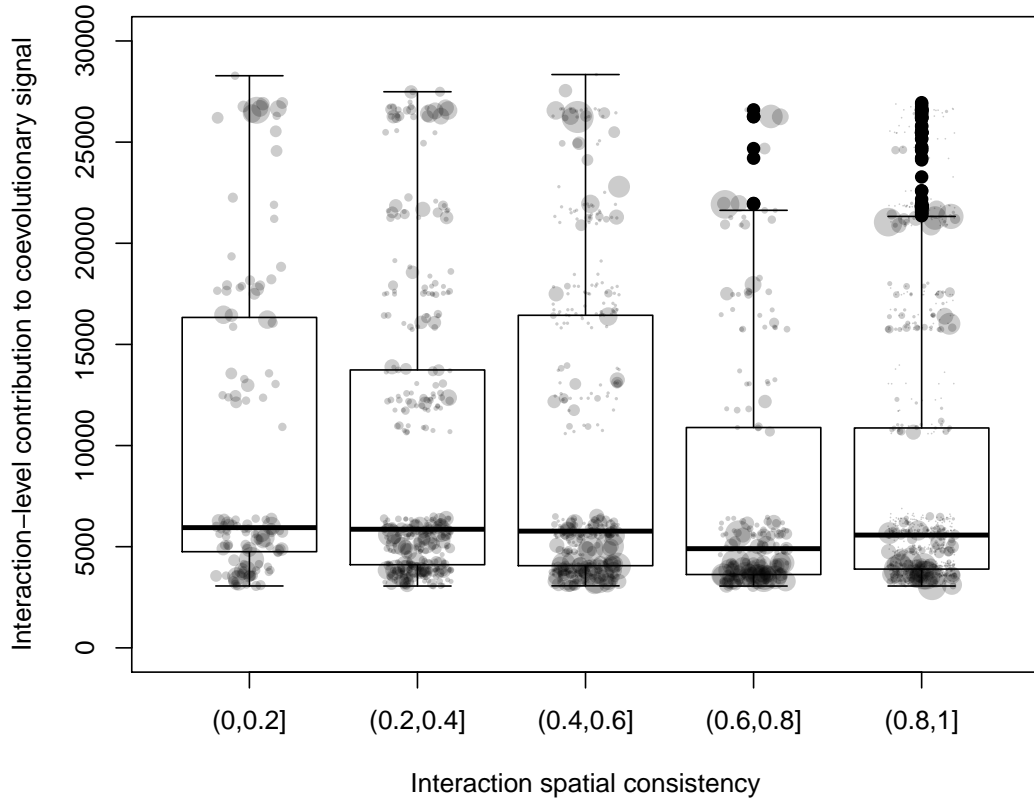


Figure 3: Spatial consistency of an interaction and its contribution to coevolutionary signal. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur. Although statistically significant, there was no meaningful relationship between spatial consistency and an interaction’s importance for coevolution in the continental network ($R^2 \approx 0.01$, $\rho = -0.1$, $p \leq 10^{-5}$).

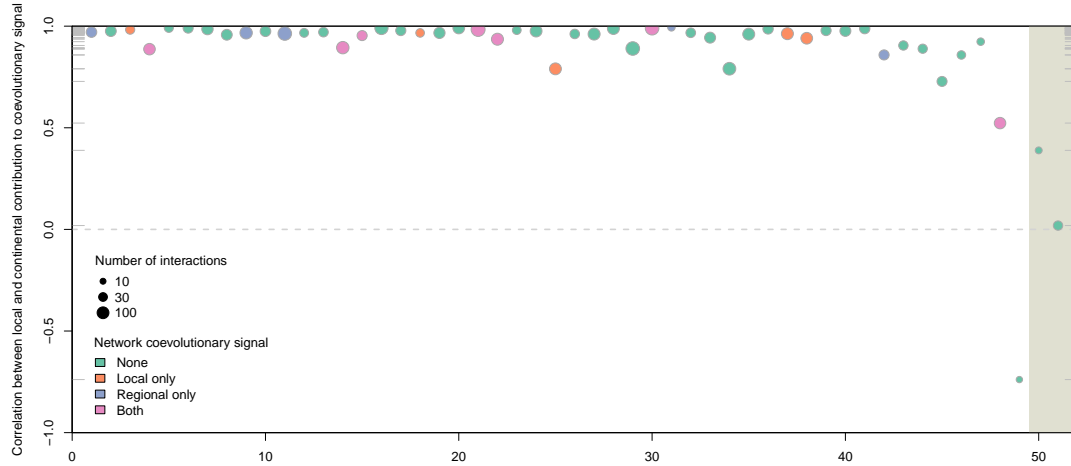


Figure 4: Correlation (Pearson’s statistic) between the interaction-level contribution to coevolutionary signal at the local and continental scales. Each dot represents one community. Communities in the shaded area have non-significant correlations ($\alpha = 0.05$).

- 1 hosts and parasites with partially overlapping geographic ranges. *J. Evol. Biol.*
- 2 **16**, 1337–1345 (2003).
- 3 6.Thompson, J. N. *et al.* *The Geographic Mosaic of Coevolution*. (University Of
- 4 Chicago Press, 2005).
- 5 7.Page, R. D. M. *et al.* *Tangled trees: Phylogeny, cospeciation, and coevolution*.
- 6 (University of Chicago Press, 2003).
- 7 8.Urban, M. C. *et al.* The evolutionary ecology of metacommunities. *Trends Ecol.*
- 8 *Evol.* **23**, 311–317 (2008).
- 9 9.Poisot, T. *et al.* in *Evolutionary Ecology of Host-Parasite Systems* (eds. Morand,
- 10 S., Littlewood, D. T. & Poulin, R.) (Cambridge University Press, 2015).
- 11 10.Jordano, P., Bascompte, J. & Olesen, J. M.*et al.* Invariant properties in co-

1 evolutionary networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).

2 11.Eklof, A., Helmus, M. R., Moore, M., Allesina, S. & Eklöf, A.*et al.* Relevance
3 of evolutionary history for food web structure. *Proc. R. Soc. B Biol. Sci.* **279**,
4 1588–1596 (2011).

5 12.Stouffer, D. B., Sales-Pardo, M., Sirer, M. I. & Bascompte, J.*et al.* Evolu-
6 tionary Conservation of Species’ Roles in Food Webs. *Science* **335**, 1489–1492
7 (2012).

8 13.Van Valen, L. *et al.* A new evolutionary law. *Evol. Theory* **1**, 1–30 (1973).

9 14.Gandon, S., Buckling, A., Decaestecker, E. & Day, T.*et al.* Host-parasite
10 coevolution and patterns of adaptation across time and space. *J. Evol. Biol.* **21**,
11 1861–1866 (2008).

12 15.Hembry, D. H., Yoder, J. B. & Goodman, K. R.*et al.* Coevolution and the
13 Diversification of Life. *The American Naturalist* **184**, 425–438 (2014).

14 16.Legendre, P., Desdevises, Y. & Bazin, E.*et al.* A statistical test for host-
15 parasite coevolution. *Syst. Biol.* **51**, 217–234 (2002).

16 17.Fahrenholz, H. *et al.* Ectoparasiten und abstammungslehre. *Zool. Anz.* **41**,
17 371–374 (1913).

18 18.Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jordano, P. & Bascompte,
19 J.*et al.* Non-random coextinctions in phylogenetically structured mutualistic net-
20 works. *Nature* **448**, 925–8 (2007).

21 19.Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D.*et al.* The
22 dissimilarity of species interaction networks. *Ecol Lett* **15**, 1353–1361 (2012).

- 1 20.Poisot, T., Stouffer, D. B. & Gravel, D.*et al.* Beyond species: why ecological
2 interaction networks vary through space and time. *Oikos* n/a–n/a (2014).
- 3 21.Data from: Phylogenetic signal in module composition and species connectivity
4 in compartmentalized host-parasite networks. (2012).
- 5 22.Verneau, O., Du Preez, L. & Badets, M.*et al.* Lessons from parasitic flatworms
6 about evolution and historical biogeography of their vertebrate hosts. *C. R. Biol.*
7 **332**, 149–158 (2009).
- 8 23.Krasnov, B. R. *et al.* Phylogenetic Signal in Module Composition and Species
9 Connectivity in Compartmentalized Host-Parasite Networks. *Am. Nat.* **179**,
10 501–511 (2012).
- 11 24.Combes, C. *et al.* *Parasitism - The Ecology and Evolution of Intimate Inter-*
12 *actions*. (University Of Chicago Press, 2001).
- 13 25.Thompson, J. N. *et al.* The raw material for coevolution. *Oikos* **84**, 5–16
14 (1999).
- 15 26.Olito, C. & Fox, J. W. *et al.* Species traits and abundances predict metrics of
16 plant–pollinator network structure, but not pairwise interactions. *Oikos* n/a–n/a
17 (2014).
- 18 27.*Biogeography of host-parasite interactions*. (Oxford University Press, 2010).
- 19 28.Cavender-Bares, J., Kozak, K. H., Fine, P. V. A. & Kembel, S. W.*et al.* The
20 merging of community ecology and phylogenetic biology. *Ecol. Lett.* **12**, 693–715
21 (2009).
- 22 29.Balbuena, J. A., Míguez-Lozano, R. & Blasco-Costa, I.*et al.* PACo: A Novel
23 Procrustes Application to Cophylogenetic Analysis. *PLoS ONE* **8**, e61048 (2013).

- ¹ 30. Ives, A. R. & Helmus, M. R. *et al.* Phylogenetic Metrics of Community Simi-
² larity. *The American Naturalist* **176**, E128–E142 (2010).